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A synthesis of life history characteristics and stock grouping of Atlantic salmon (*Salmo salar* L.) in eastern Canada

Synthèse des caractéristiques biologiques et regroupement des stocks de saumon atlantique (*Salmo salar* L.) de l'est du Canada

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Canada

Foreword

This document is a product from a workshop that was not conducted under the Department of Fisheries and Oceans (DFO) Science Advisory Process coordinated by the Canadian Science Advisory Secretariat (CSAS). However, it is being documented in the CSAS Research Document series as it presents some key scientific information related to the advisory process. It is one of a number of contributions first tabled at a DFO-SARCEP (Species at Risk Committee / Comité sur les espèces en péril) sponsored workshop in Moncton (February 2006) to begin the development of a 'Conservation Status Report' (CSR) for Atlantic salmon. When completed in 2007, the CSR could form the basis for a Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status report, recovery potential assessment and recovery strategy, and most importantly, enable DFO to implement pre-emptive management measures prior to engagement in any listing process.

Avant-propos

Le présent document est issu d'un atelier qui ne faisait pas partie du processus consultatif scientifique du ministère des Pêches et des Océans, coordonné par le Secrétariat canadien de consultation scientifique (SCCS). Cependant, il est intégré à la collection de documents de recherche du SCCS car il présente certains renseignements scientifiques clés, liés au processus consultatif. Il fait partie des nombreuses contributions présentées au départ lors d'un atelier parrainé par le MPO-SARCEP (Species at Risk Committee / Comité sur les espèces en péril) à Moncton (février 2006) en vue de commencer l'élaboration d'un rapport sur la situation de la conservation du saumon atlantique. Lorsqu'il sera terminé, en 2007, ce rapport pourrait servir de base à un rapport de situation du Comité sur la situation des espèces en péril au Canada (COSEPAC), à une évaluation du potentiel de rétablissement et à un programme de rétablissement mais, avant tout, il permettra au MPO de mettre en œuvre des mesures de gestion anticipées avant même de s'engager dans un processus d'inscription.

Abstract

This document summarizes geographically the available information for selected phenotype characteristics of wild Atlantic salmon (*Salmo salar* L.) adults from 112 rivers in eastern Canada. The variations in biological characteristics described support many of the previous analyses of geographic variation of phenotype in Atlantic salmon. Age at smoltification has a significant positive association with latitude with the additional feature that mean age also increases along a west to east gradient. There are important differences in the characteristics of stocks of Newfoundland from the other areas in eastern Canada, differences primarily in smolt ages of Labrador origin salmon and differences in some characteristics of salmon from rivers at the southern edge of the distribution. The characteristics of many stocks show similarities which override the provincial and management boundaries. When small and large salmon characteristics are combined, four broad groups are defined: Gulf of St. Lawrence including some rivers of southwest Newfoundland, Maritime provinces including some rivers of the southern Gulf, insular Newfoundland, and Labrador. Some biological characteristics of the Atlantic coast of Nova Scotia rivers, such as the proportion female and fork length of small salmon, are more similar to the Newfoundland rivers' characteristics than to those from the other rivers of the Maritime provinces. Variations in the adult salmon characteristics related to the age, size and sex ratios of the maturing adult salmon have fitness consequences for the salmon stocks.

Résumé

Dans le présent document, les caractéristiques du genre phénotype prélevés d'adultes de saumon atlantique sauvage provenant de 112 rivières de l'est du Canada sont présentées sous un aspect géographique. Les variations observées de ces caractéristiques confirment plusieurs des analyses antérieures par rapport à la variabilité géographique du caractère phénotype du saumon atlantique. L'âge à smoltification est positivement associé à la latitude avec une association secondaire d'augmentation de l'âge moyenne passant de l'ouest à l'est. Il y a des différences importantes dans les caractéristiques des stocks de saumon dans les rivières de Terre-Neuve par rapport aux autres endroits de l'est du Canada. Ces différences se manifestent principalement dans l'âge à smoltification des saumons du Labrador et des différences des caractéristiques par rapport aux stocks dans les zones plus au sud. Les similarités des caractéristiques de plusieurs stocks s'étendent au-delà des frontières provinciales et des zones de gestion. On peut distinguer quatre regroupements de populations par rapport aux caractéristiques des petits saumons et des grands saumons. Un premier groupe comprend les rivières du Golfe du Saint-Laurent et quelques rivières du sud-ouest de Terre-Neuve. Un deuxième groupe comprend les rivières des provinces maritimes et quelques rivières du sud du golfe. Les rivières de Terre-Neuve et celles du Labrador comprennent les troisième et quatrième regroupements. Pour certaines caractéristiques telles que la proportion femelle et la longueur moyenne des petits saumons, les similarités sont plus importantes entre les rivières de Terre-Neuve et de la côte atlantique de la Nouvelle-Écosse qu'entre ce dernier et les autres rivières des provinces maritimes. Les variations de caractéristiques des saumons adultes associées à l'âge, la taille et la proportion de femelle ont des conséquences importantes sur l'adaptation évolutive des stocks.

INTRODUCTION

Atlantic salmon (*Salmo salar* L.) displays plasticity in phenotypes across its species range. Geographic variations in growth rates, age at smoltification, age at first maturity, size at maturity and sex ratios have been summarized in numerous reviews (O'Connell et al. 2006; Klemetsen et al. 2003; Hutchings et al. 1998). The variability in these phenotypes reflects a combination of genotype and environment influences. It seems likely that age at smoltification for example would be strongly under the control of environmental factors as there is a demonstrated inverse relationship between mean age at smoltification and latitude as well as between growth rate of juveniles and age at smoltification (Metcalfe and Thorpe 1990; Strothotte et al. 2005). On the other hand, sea-age at maturity appears to be strongly influenced by parental stock as shown by the relationship between ovarian development of migrating smolts and age at maturity of adult spawners (Chadwick et al. 1986, 1987), selective breeding of broodstock for late maturation (Glebe and Saunders 1986), and recent thoughts on precocious male maturation influencing subsequent age at maturity of male progeny (Duston et al. 2005).

Molecular genetics addresses the extent of reproductive isolation of salmon among and within rivers and there is increasing evidence for existence of adaptation on different geographical scales. Adaptation in this sense refers to the matching of phenotype and environment with adaptive variation arising from heritability of phenotypic traits, variation at the molecular level, and plasticity of phenotypes resulting from the interaction of the genes and the environment (Garcia de Leaniz et al. 2006).

Variations in phenotype of Atlantic salmon among rivers and broad geographic areas are essential but insufficient evidence of adaptation because of the plasticity of phenotype resulting from the genetic and environmental interactions (Hutchings and Jones 1998). Nevertheless, characterization of the variations in phenotype and analysis of groups of rivers with similarities in multiple characteristics provide insights into the geographic distribution of Atlantic salmon stocks which express similar phenotypes and possibly similar adaptations. The analysis of phenotypic variation in Atlantic salmon in eastern Canada contributes to the discussion regarding conservation units or evolutionarily significant units within the context of initiatives within Canada on the conservation of species and biodiversity (Committee on status of Endangered Wildlife in Canada (COSEWIC) and Species at Risk Act (SARA)). As well, the analysis of phenotype is of interest as these external features are used to define how the resource is exploited and managed.

This document summarizes the available information for selected phenotype characteristics of wild Atlantic salmon adults from rivers in eastern Canada. The data were taken from Department of Fisheries and Oceans (DFO) and the province of Quebec data sets. The characteristics of interest include proportions at smolt age by size and sea age group, sea age at maturity, fork length at sea age, proportion female in sea age groups and proportion by sea age group. The characteristics are summarized geographically and multiple characteristics are used to delineate stock groupings.

MATERIALS AND METHODS

Biological information from 112 rivers in eastern Canada was provided by staff from DFO regions in Newfoundland and Labrador, Maritimes and Gulf as well as biologists from the province of Quebec (Fig. 1). Salmon were sampled from catches at counting fences, fishways, from broodstock sampling, and estuarine trapnets. These samples were augmented by opportunistic sampling from fisheries catches.

Sample sizes and temporal coverage varied among rivers. In some rivers, information was available from only one or two years but for about 50% of the rivers, 6 or more years of sampling information was

available. For fourteen rivers, information was available for more than 25 years with the Miramichi River having the longest time series of information at 35 years.

Number of years	Number of rivers	Percentage of total
1 to 2	20	18%
3 to 5	37	33%
6 to 10	21	19%
11 to 20	20	18%
> 20	14	13%
Total	112	

Time periods sampled have varied among rivers and in the interest of obtaining the widest spatial coverage possible, we accepted biological characteristics information from any available time period.

For purposes of analysis, the following terms are used.

- smolt – juvenile salmon on their first migration to the ocean after having spent one to more years in fresh water
- small salmon – adult salmon < 63 cm fork length regardless of sea age
- large salmon – adult salmon >= 63 cm fork lengths regardless of sea age
- maiden salmon – adult salmon on a first spawning migration regardless of sea age
- 1SW – one sea winter salmon are adult salmon which have spent one year at sea regardless of size
- 2SW – two sea winter salmon are adult salmon which have spent two years at sea without spawning, regardless of size
- 3SW – three sea winter salmon are adult salmon which have spent three years at sea without spawning

The biological characteristics of interest included smolt age, proportion of returns by size group, proportion maiden salmon by size group, proportions of maiden sea ages, proportion female by size group and within the maiden sea age groups, and mean fork length of size group and of maiden sea age groups (Table 1). River-specific mean values over all years and samples were used.

The entire suite of biological characteristics was not available from all the rivers (Table 1). Scale sampling and interpretation of scales are required to determine smolt age and sea age. Ideally, the proportions at smolt age and by maiden sea age would represent the average proportions for a cohort. This information was available from a very small number of rivers and instead, proportions within annual sampling were used. Proportion of returns which are small salmon requires an estimate of total run size of small salmon (< 63 cm fork length) and large salmon (>= 63 cm fork length). Proportion of maiden fish overall requires scale sampling and estimates of overall run size of each size component (small salmon, large salmon) whereas proportion maiden fish by size group requires only representative sampling within each size group. Proportion of maiden sea ages in the runs requires sampling for age as well as estimates of total abundance to the river.

Proportion by smolt age of small salmon was the most widely available characteristic (N = 108) followed by mean fork length of small salmon (Table 1). In most rivers of Newfoundland and Labrador, biological characteristics of small salmon were assumed to correspond to characteristics of 1SW maiden salmon as the majority of salmon in the small size category are maiden 1SW fish (Dempson et al. 2004). Characteristics of 3SW maiden fish were the rarest because 3SW maiden salmon have a restricted distribution in eastern Canada, and they are less abundant than the other age groups and can be missed in limited sampling programs.

Analysis of stock groupings

Dimension reduction methods (principal components analysis) and cluster analysis were used to explore the similarities among rivers based on combinations of biological characteristics. For the proportion at smolt age characteristics, the proportion at age 1 was not used and the proportions at ages 6 and 7 were transformed to a single binary variable indicating presence (1) absence (0) of any of those age groups in the river.

Principal components analysis was first applied to the selected suite of variables and a reduced set of components was retained for cluster analysis. The principal components analysis was run using SAS Proc PRINCOMP, using the correlation matrix option.

The number of principal components retained in the cluster analysis was taken as the number of components which accounted for a minimum of 70% of the variance. The cluster analysis was conducted using SAS Proc Cluster with the average distance metric to define groups. A cluster tree was drawn using SAS Proc Tree.

We analyzed the similarities among rivers for three combinations of size groups of fish:

1) small salmon characteristics. The variables examined included proportion at smolt age of small salmon, proportion female, and mean length (7 variables) represented in 92 rivers. When proportion at smolt age for small salmon was not provided, the proportion at smolt age for 1SW salmon was used. If mean length of small salmon or proportion female in small salmon were not provided, the corresponding values from 1SW salmon were used.
2) large salmon characteristics. The variables examined included proportion at smolt age of large salmon, proportion female, and mean length (7 variables) represented in 76 rivers. If proportion at smolt age for large salmon was not provided, the proportion at smolt age for 2SW salmon was used. If mean length of large salmon or proportion female in large salmon were not provided, the corresponding values from the average for 2SW and 3SW salmon were used.
3) small and large salmon characteristics. The variables examined included smolt age of salmon, proportion female in small salmon and large salmon, mean length of small salmon and large salmon, proportion of returns which are small, and proportion maiden in total returns (10 variables) represented in 47 rivers. In this analysis, none of the rivers retained had smolt ages greater than 5 years therefore the binary variable for smolt age 6 and 7 was not used. The proportion at smolt age was taken as proportion for all size or age groups when provided, else the proportion in small salmon was used, else the proportion in large salmon was used. For proportion maiden in total returns, where this was not provided, the product of the proportion returns small and the corresponding proportion maiden in small and proportion maiden in large was used.

RESULTS

The rivers from eastern Canada with biological characteristics information represent a wide geographic coverage including 31 rivers from the Maritime provinces (18 rivers from the DFO Maritimes Region, 13 rivers from DFO Gulf Region), 26 rivers from the province of Quebec, and 55 rivers from DFO Newfoundland and Labrador Region (Fig. 1). The most southerly river in the data set is located at Lat. 43.9°N (Tusket River, Nova Scotia) with the most northern river at Lat. 55.6°N (Hunt River, Labrador) (Fig. 1).

Proportions at smolt age for either small salmon, large salmon or combined sea age groups are available from 112 rivers with proportions at smolt age of small salmon available from 108 rivers. The 3SW

maiden salmon characteristics are defined from 17 rivers with smolt age distributions from this age group available from 11 rivers (Table 1). Complete information for small salmon (smolt age distributions, mean fork length, proportion female) is available from 92 rivers whereas similar complete information for large salmon is available for 74 rivers. Combined information for small and large salmon, including smolt age distribution (all age groups, small salmon or large salmon as indicator), mean length (small, large), proportion female (small, large), proportion of total returns which are small, and proportion of total returns which are maiden fish are available from 47 rivers (Table 1).

Smolt age

Reported smolt ages range from one to seven years and mean age increases with latitude (Fig. 2, 3). Age two-year old smolts are abundant in the Maritime provinces as well as some rivers of Quebec and Newfoundland but are rare in Labrador (Fig. 2a, 2b). Age three-year old smolts have been sampled from all rivers with the exception of Middle Brook (SFA 1) in Labrador. Age six-year old smolts are found in some rivers of the north coast of Newfoundland (SFA 4, 5), Labrador and the north shore of Quebec, bordering Labrador (Fig. 2a, 2b). With the exception of a report from Campbellton River (SFA 4), age 7-year old smolts have only been found in Labrador. Smolt age distributions of large salmon are available from 87 rivers and show a similar latitudinal association to that for small salmon (Fig. 2a). A large proportion (0.83) of the variation in mean age is explained by latitude and longitude with mean age increasing from south to north and from west to east (Fig. 3; Table 2). As single variables, latitude explains a larger proportion of the variance in mean smolt age than longitude, 0.71 versus 0.26, respectively. Combined, latitude accounts for an additional 68% of the explained variance whereas longitude explains an additional 15% (Table 2).

The presence of one-year old smolts is reported from 17 rivers, mostly from the Maritime provinces (SFA 19 to 23). A total of nine rivers in SFA 19 to 23 have varying percentages of one-year old smolts, ranging from a low of 0.2% in Grand River (SFA 19) to a high of 34.7% in Tusket River (SFA 21). In other regions, one-year smolts are reported from one river in Labrador (0.3% from English River, SFA 1), two rivers in Newfoundland (0.4% and 0.1%, respectively, Conne and Little River, SFA 11), and five rivers in Quebec (3.7% in Bonaventure Q1, 26.8% in Petit Pabos, 0.6% in Grande Rivière, <0.1% in St. Jean Q2, 0.1% in de la Trinite Q7). One-year old wild smolts are unlikely in rivers north of SFAs 20 to 23. One-year old hatchery smolts may have been stocked in some of these rivers and mis-identified as wild origin. Alternatively, one-year old smolt data could be the result of mis-interpretation of age from the scales.

Proportion female

Estimates of the proportion female are available from 96 rivers for small salmon and 76 rivers for large salmon (Table 1). There are important differences in the proportion female within the small salmon size group among rivers in eastern Canada (Fig. 4a). The proportion female increases from west to east. Small salmon are predominately male in rivers of the southern Gulf of St. Lawrence, Quebec and many rivers of Labrador. In contrast, small salmon are mostly female in the rivers of insular Newfoundland with the exception of a few rivers in the southwest coast (SFA 13) (Fig. 4a). Within Newfoundland, stocks from the east coast have a higher proportion female than the stocks from the west coast and northern peninsula (Fig. 4a). Small salmon are about 50% female in the rivers of the Atlantic coast of Nova Scotia and the many small rivers of SFA 13 in southwest Newfoundland. The characteristics of these southern stocks are more similar to the west Newfoundland characteristics than to the rivers from the Maritimes in the southern Gulf.

Large salmon are mostly female in all areas of eastern Canada with the exception of some rivers along the north shore of the St. Lawrence and Gaspe area in Quebec, where the ratio of males and females is nearly equal (Fig. 4b).

By maiden sea age group, the proportion female is available from 96 rivers for 1SW salmon, 45 rivers for 2SW salmon and 13 rivers for 3SW salmon. For many rivers of Newfoundland, the proportion female in the 1SW salmon is identical to that of small salmon since most small salmon are 1SW maiden fish (Fig. 4c). In most rivers, 2SW salmon are about 72% female (median value), ranging from 32% to 100% (Table 1; Fig. 4c). There is wide variation in the proportion female in 3SW salmon, ranging from 0.04 to 1.0, with generally more females than males, but samples sizes for this age group are small (Table 1; Fig. 4c).

Mean length

Estimates of mean fork length of small salmon and large salmon are available from 104 and 88 rivers, respectively (Table 1). With few exceptions, the shortest mean length (cm) for small salmon is in the rivers of insular Newfoundland whereas the longest small salmon are in north shore St. Lawrence rivers (Zones Q7 to Q9) (Fig. 5a). The shortest large salmon, at mean fork lengths between 63 and 68 cm, are also found in rivers of insular Newfoundland (Fig. 5b). The longest large salmon are found in the rivers of the southern Gulf of St. Lawrence and Quebec.
The mean lengths of 1SW maiden salmon, available from 101 rivers, show similar geographic variation as small salmon (Fig. 5c). Data on mean fork lengths of 2SW maiden salmon are available from 76 rivers. The longest 2SW salmon are in the rivers of the southern Gulf and Quebec and in some rivers of Labrador. The shortest 2SW salmon are in some of the rivers in the north shore of the St. Lawrence, Anticosti Island (Q10) and in the few rivers of insular Newfoundland where 2SW maiden salmon are found (Fig. 5c). In most rivers, 3SW maiden salmon have mean fork lengths of about 90 cm, the few exceptions being in rivers where sample sizes are small (Fig. 5c).

Proportion small salmon in total returns

The relative abundance of small salmon and large salmon in the total returns to rivers is available from 72 rivers in eastern Canada (Table 1). Small salmon comprise greater than 75% of the total returns in the majority of rivers in insular Newfoundland, Labrador and in the Atlantic coast of Nova Scotia (Fig. 6). With few exceptions, large salmon are more abundant than small salmon in rivers of the southern Gulf of St. Lawrence and eastern Cape Breton Island (SFA 19) (Fig. 6). There are variations to these general characteristics in all areas.

Proportion maiden salmon

Data relative to the maiden versus repeat spawning age structure are available from 30 rivers for the total returns, from 70 rivers for small salmon and from 50 rivers for large salmon. The proportion maiden in small salmon is generally above 0.9 (83% of sampled rivers) with repeat spawning salmon more common in the small salmon size category in rivers of insular Newfoundland (Fig. 7a). In the Maritime provinces, Quebec and Labrador, small salmon are essentially maiden one-sea-winter salmon (1SW) (Fig. 7a).

The proportion maiden salmon in the large salmon category is much more variable than for small salmon, ranging from less than 0.1 to almost 1 (Fig. 7b). Maiden salmon are a small proportion of the large salmon group in rivers of insular Newfoundland with the exception of those along the southwest coast (Fig. 7b). There are two distinct groupings of rivers in eastern Canada; one group is characterized by low proportion maiden in the large salmon (< 0.40), the other group by a high proportion maiden (>0.60) (Fig. 7c). In terms of the percentage maiden salmon in the total returns, several rivers in Newfoundland and in

the inner Bay of Fundy have less than 75% maiden salmon and several other rivers in Newfoundland and a few in the Maritimes have less than 85% maiden salmon (Fig. 7d). Otherwise, maiden salmon comprise greater than 85% of the returns of salmon, all size and age groups (Fig. 7d).
Proportions at maiden sea age are available from 17 rivers. The sea age-at-maturity composition is highly variable among rivers, ranging from 9% to 85% for one-sea-winter sea-age, 15% to 90% for two-sea-winter sea age, and 0 to 11% for three-sea-winter sea age (Fig. 8). The highest proportions of 2SW salmon are found in the Gulf rivers of Nova Scotia (SFA 18).

Dimension reduction and groupings of rivers

Principal components analysis followed by cluster analysis are used to identify groups of rivers with shared biological characteristics. Three analyses are performed: the first for small salmon characteristics, the second for large salmon characteristics, and the third using characteristics of small and large salmon simultaneously.

Small salmon analysis

A total of 92 rivers have complete information for the seven biological characteristics of interest (Table 1, 3). Sixty-four percent of the variance is explained by the first two principal components, and 77% of the variance is explained with the first three components (Table 3). The weights on the first component are most important for the proportion at smolt age 2 and 3 years (- correlation) as opposed to the proportions smolt age 4 and smolt age 5 years as well as the presence of smolt age 6-7 years (+ correlation) (Table 3). Weights on the second component are highest for proportion smolt age 3 and the proportion female (-) in opposition to the proportion smolt age 2 years and mean length (Table 3). The weights on third component are highest on the proportion smolt age 4 years (-) as opposed to the presence of smolts aged 6 or 7 years (Table 3).

There is a clear separation of Labrador rivers from all other regions on the first component whereas the second component separates the rivers of insular Newfoundland from most of the mainland rivers (Fig. 9). Rivers from zone Q10 (Anticosti Island) are closest to Newfoundland rivers while rivers in zone Q9 are closest to the Labrador rivers (Fig. 9). The Maritimes separates from the Quebec rivers on the first component with overlap in Q7 and southern Gulf NB rivers.

Based on the first three principal components, twenty-seven rivers of the Maritime provinces and the southern zones of Quebec (Q1 to Q7) cluster together (Fig. 10a, 10b). Thirty-six rivers, mostly from insular Newfoundland, form a second group with a few rivers in the mid-latitude of Quebec (zones Q8 and Q10) (Fig. 10b). A third group of 22 rivers includes some rivers from the northeast coast, northern peninsula of Newfoundland with the northern rivers of Quebec and a few rivers from Labrador, with a fourth cluster of five rivers uniquely from Labrador (Fig. 10a, 10b). Two rivers from insular Newfoundland (Exploits, Campbellton) cluster together and join the Labrador cluster before the other rivers. These rivers are unique for insular Newfoundland in that smolts aged 6 or 7 years have been found there yet they have a high proportion of three year old smolts which differs from the Labrador rivers (Appendix 1).

Large salmon analysis

A total of 74 rivers have complete information for the seven biological characteristics of interest (Table 1, 4). Whereas 56% of the variance could be explained by the first two principal components, a total of 75% of the variance was accounted for with the first three components (Table 4). The weights on first component are most important for the proportion at smolt age 2 years (-) as opposed to the

proportions smolt age 4 and smolt age 5 years (+) (Table 4). Weights on the second component are highest for proportion smolt age 3 as opposed to the proportion at smolt age 2 years (Table 4). The weights on third component are highest on the proportion female as opposed to mean length (Table 4).

There is a clear separation of Maritime provinces rivers from Labrador on the first component and from Newfoundland rivers on the second component (Fig. 11a, 11b). The Maritimes provinces rivers separate from the Quebec rivers on the first component with overlap in Q7 and southern New Brunswick rivers (SFA 16, 23) (Fig. 11a, 11b).

Based on the first three principal components, twenty-six rivers of the Maritime provinces and the upper north shore of Quebec (Q6 and Q7) cluster together (Fig. 12a, 12b). Twenty-six rivers, mostly from insular Newfoundland, form a second group with a few rivers in the mid-latitude of Quebec (zones Q1, Q2, Q7 to Q10) and northeast Nova Scotia (SFA 19) (Fig. 12b). A third group of 12 rivers includes mostly rivers from Quebec Gaspe area and the lower north shore (Zone Q8) as well as one river from southwest Newfoundland (Highlands River) (Fig. 12b). With the exception of one river, all the Labrador rivers cluster together with a few rivers from Quebec Zone Q9 (Fig. 12a, 12b). One river forms its own cluster (Sand Hill River) because it is the only river which has smolt age 6-7 years present in the large salmon category (Fig. 12a; Appendix 2).

Combined small and large salmon characteristics

A total of 47 rivers had information for the ten biological characteristics of interest (Table 1, 5; Appendix 3). Fifty-nine percent of the variance is explained by the first two principal components, increasing to 73% of the variance with the first three components (Table 5). The weights on first component are most important for the proportion female in small salmon and proportion of returns which are small salmon as opposed to the mean length of large salmon (Table 5). Weights on the second component were highest for proportion smolt age 5 and 4 years as opposed to the proportion at smolt age 3 years (Table 5). The weights on third component were highest on the proportion at smolt age 3 as opposed to the proportion at smolt age 2 (Table 5).

There is a clear separation of Gulf Region rivers from Newfoundland rivers on the first component and Labrador rivers from all other rivers on the second component (Fig. 13a). The Quebec rivers overlap the rivers of the Maritime provinces and Newfoundland along the first component with the river in zone Q2 overlapping with Gulf rivers and those of zone Q10 closest to Newfoundland rivers (Fig. 13b).

There are about five clusters which can be distinguished for this set of 47 rivers (Fig. 14a). The southern Gulf of St. Lawrence rivers cluster with the Quebec rivers and with one of the rivers in southwest Newfoundland (SFA 13) (Fig. 14a, 14b). Some southern Gulf rivers cluster with a group of rivers from the Bay of Fundy and the Atlantic coast of Nova Scotia. A closely related cluster groups rivers from the inner Bay of Fundy with some rivers from the Atlantic coast of Nova Scotia (Fig. 14b). Newfoundland forms a distinct cluster as does Labrador (Fig. 14a, 14b).

DISCUSSION

The phenotypic characteristics of the adult salmon are of greatest interest because these are the features which are valued in fisheries (Porter et al. 1986). Size increases with sea age and in most fisheries, the larger fish are the most desired. Since fecundity also increases with size (O'Connell et al. 2006), larger fish contribute a larger number of eggs at spawning and size may influence spawning success (Fleming

1998). Age at maturity and size at maturity characteristics are therefore of particular interest (see Meerburg 1986).

The variations in biological characteristics described in this document support many of the previous analyses of geographic variation of phenotype in Atlantic salmon. The age at smoltification has a significant positive association with latitude with the additional feature that mean age also increases along a west to east gradient (Metcalfe and Thorpe 1990; O'Connell et al. 2006; Klemetsen et al. 2003). This variation is largely determined by growth conditions, primarily temperature and photoperiod, which are favourable in the southern latitudes and constrained in the northern areas. The longitudinal cline reflects the mediating influence of the Atlantic Ocean on climate and those rivers at the eastern edge of Canada are influenced by the cooling effect of the ocean, resulting in slower growth and older age at smoltification. Although age at smoltification is generally attributed to be mostly under the influence of the environment, there is evidence that growth rates which affect age at smoltification may be heritable. Nicieza et al. (1994) conducted a common garden experiment with a northern stock (Scotland) and southern stock (Spain) grown under conditions of the southern stock and found that growth rate in the first summer was higher for the northern stock but the proportion of fish which smoltified after one year was higher for the southern stock. They attributed this to the threshold size needed to trigger smoltification being higher for the northern population. If threshold size and growth rates are stock specific, then the observed variation in age at smoltification noted for eastern Canada may reflect more than the influence of environmental conditions.

Small salmon are the dominant component in the returns to rivers in large portions of insular Newfoundland whereas the Maritime, Quebec and Labrador rivers have important contributions of large salmon. Porter et al. (1986) referred to Type I stocks which are mostly 1SW salmon and these in turn have a high proportion female. This contrasts with the Type II stocks which have important 2SW maiden salmon and a much lower proportion of females in the 1SW component. Type II stocks contain 2SW and 3SW spawners and a very low proportion female in the 1SW component. These geographic groupings were confirmed in this analysis.

In addition, we noted important differences in the characteristics of stocks of Newfoundland from the other areas in eastern Canada, differences primarily in smolt ages of Labrador origin salmon relative to other areas and differences in some characteristics of salmon from the rivers at the southern edge of the distribution along the Atlantic coast of Nova Scotia and the inner Bay of Fundy. For Newfoundland, the following characteristics are particularly notable: small salmon and large salmon are generally of shorter length, small salmon have a high proportion female, small salmon have some repeat spawners within the size group, and large salmon are mostly repeat spawners. The Gulf of St. Lawrence stocks including those from the Maritimes and Quebec, share a number of characteristics including: few to no repeat spawners in the small salmon category, an abundance of large salmon in the total returns to the rivers, long (in length) small salmon and large salmon, and low proportions female in the small salmon category.

The characteristics of many stocks show similarities which override the provincial and management boundaries. For example, several rivers of the southwest coast of Newfoundland (SFA 13) share characteristics which are more similar to the Maritime and Quebec stocks than to the Newfoundland stocks. Also, stocks from Anticosti Island (Q10) have some characteristics (fork length of small salmon and large salmon) which are closer to those of insular Newfoundland than to the Gulf of St. Lawrence mainland stocks. Labrador stocks share characteristics with those of the Quebec north shore (Q9) in terms of smolt age, and proportion female in the small salmon.

The small salmon component of rivers of eastern Canada can be characterized into three groups following an approximate latitudinal gradient. The rivers of the Maritimes and the upper St. Lawrence of Quebec

form one group with shared characteristics (youngest ages at smoltification, long small salmon, low proportion female in small salmon). The rivers of insular Newfoundland cluster with the stocks in Quebec in zones Q8 and Q10 and are characterized by smolt ages of 3 to 4 years. The northern rivers in Labrador, zone Q9 in Quebec and some rivers from the northern peninsula of Newfoundland are characterized by older smolt ages.

Large salmon can be characterized into four groups: one group from the Maritime provinces and the upper St. Lawrence, a second group from the Gaspe region of Quebec and the north shore (Q8), a third group consisting of insular Newfoundland, Anticosti Island (Q10) and the eastern north shore of the St. Lawrence (Q8, Q9) and a final group for Labrador and part of zone Q9. Smolt age is an important characteristic that distinguishes these groups but the longitudinal separation of Quebec and Newfoundland is determined by the gradient in length and the proportion female of the large salmon.

When small and large salmon characteristics are combined, four broad groups are defined: Gulf of St. Lawrence including some rivers of southwest Newfoundland, Maritime provinces including some rivers of the southern Gulf, insular Newfoundland, and Labrador.

Verspoor (2005) presented a review of allozyme loci variation of Atlantic salmon from 53 rivers of eastern Canada. The genetic profiles showed large overlap geographically with exception to the Labrador/Ungava rivers. Based on geography and genetics, Verspoor (2005) suggested that there were six regional groups within eastern Canada: Labrador/Ungava, Gulf of St. Lawrence, Newfoundland (excluding those from Gulf Newfoundland), Atlantic coast of Nova Scotia, inner Bay of Fundy, and outer Bay of Fundy. He also mentioned the presence of intermediates such as some rivers from western Newfoundland which are intermediate between Gulf of St. Lawrence and the rest of Newfoundland as well as rivers from the Avalon Peninsula of Newfoundland which were more similar to rivers from the Atlantic coast of Nova Scotia. In our analysis of phenotype, several rivers from western Newfoundland share characteristics with those from the mainland Gulf of St. Lawrence. In addition, some characteristics of the Atlantic coast of Nova Scotia rivers, such as the proportion female and fork length of small salmon, are more similar to the Newfoundland rivers characteristics than to those from the other rivers of the Maritime provinces.

Of most interest are the variations in the adult salmon characteristics related to the age, size and sex ratios of the maturing adult salmon. Variations in these characteristics have fitness consequences for the salmon stocks and the relative roles of environment versus genetics, as determining factors in their expression, is an important area of research. There are conflicting views on the importance of environmental conditions at sea in determining sea age at maturity (Dempson et al. 1986; Friedland 1998; Hutchings and Jones 1998) whereas there is substantial evidence that sea age at maturity and other adult characteristics are heritable (Chadwick et al. 1987; Duston et al. 2005; Glebe and Saunders 1986; Gross 1998; Ritter et al. 1986). Some of these characteristics, for example proportion female by sea age group, are temporally stable within individual stocks (Hutchings and Jones 1998; O'Connell et al. 2006) whereas other characteristics, particularly fork length at age and the proportion repeat spawners, may change over time as a result of changes in fisheries exploitation (Hutchings and Jones 1998; Klemetsen et al. 2003; Moore et al. 1995; O'Connell et al. 2006). There are several rivers within eastern Canada for which annual sampling for all the biological characteristics examined in this study has been conducted. A more extensive analysis of the temporal and spatial variations of these life history characteristics, combined with genetic characterization of these rivers would be useful.

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Table 1. Summary of life history characteristics examined and the number of rivers for which data were available.

Descriptor	Number of rivers with information	Median (Min – Max.)	Number of rivers with combined information		
			92	74	47
Proportion at smolt age					
Small	108	1 to 7 years[1]	X		X
Large	87	1 to 7 years[1]		X	
1SW	48	1 to 7 years[1]			
2SW	45	1 to 5 years[1]			
3SW	11	2 to 5 years[1]			
Proportion of returns which are small salmon	72	0.82 (0.08 - 0.98)			X
Proportion which are maiden spawners					
Overall	30	0.93 (0.60 - 0.99)			
Small	70	0.99 (0.61 – 1.0)			X
Large	50	0.80 (0 - 0.98)			
Proportion of maiden spawners which are					
1SW	17	0.50 (0.09 - 0.85)			
2SW	17	0.49 (0.15 - 0.90)			
3SW	17	<0.01 (0 - 0.11)			
Proportion female in					
Small	96	0.52 (0.0 – 1.0)	X		X
Large	76	0.72 (0.47 – 1.0)		X	X
1SW	96	0.52 (0.0 – 1.0)			
2SW	45	0.72 (0.32 – 1.0)			
3SW	13	0.80 (0.04 – 1.0)			
Mean fork length (cm) of					
Small	104	54.0 (49.3 - 58.7)	X		X
Large	88	74.6 (63.5 - 95.7)		X	X
1SW	101	54.2 (48.4 - 58.7)			
2SW	76	74.1 (60.5 – 86.1)			
3SW	17	88.8 (77.9 - 101.5)			

[1] refers to the range of smolt ages for the size or sea age group

Table 2. Analysis of variance of association of mean smolt age and geographic position (latitude, longitude) of sampled rivers in eastern Canada. Mean smolt age (taken as mean age of smolts of all sea age groups when available, otherwise, small salmon are used if available, else large salmon are used).

N = 108

	Mean	Min.	Max.
Latitude °N	48.51	43.86	55.57
Longitude °W	-60.19	-69.41	-53.16
Mean age (years)	3.14	1.91	5.05

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	37.5961	18.798	262.46	<.0001
Error	105	7.5205	0.0716		
Corrected Total	107	45.1167			

R-Square	Coeff Var	Root MSE
0.833	8.52	0.267

Source	DF	Type III Sum of Squares	F Value	Pr > F
Latitude	1	25.667	358.36	<.0001
Longitude	1	5.593	78.08	<.0001

Parameter	Estimate	Standard Error	t Value	Pr > |t|
Intercept	-3.66	0.695	-5.26	<.0001
Latitude	0.205	0.011	18.93	<.0001
Longitude	0.053	0.006	8.84	<.0001

Table 3. Summary of principal components dimension reduction analysis for small salmon characteristics.

N = 92 rivers
Variables = 7

Component	Eigenvalue	Variance explained Proportion	Cumulative
1	2.5207	0.360	0.360
2	1.9634	0.281	0.641
3	0.9389	0.134	0.775
4	0.8193	0.117	0.892
5	0.5512	0.079	0.971
6	0.1970	0.028	0.999
7	0.0095	0.001	1.000

Weights of variables by eigenvector			
	Eigenvector		
	1	2	3
Smolt age 2	-0.3621	0.4482	0.1053
Smolt age 3	-0.3812	-0.4140	0.2414
Smolt age 4	0.4866	-0.2055	-0.5375
Smolt age 5	0.5506	0.2366	0.1516
Smolt age 6-7	0.4082	0.1523	0.6942
Prop. female	0.1160	-0.5038	0.0274
Mean length	-0.0588	0.5025	-0.3690

Table 4. Summary of principal components dimension reduction analysis for large salmon characteristics.

N = 74 rivers
Variables = 7

Component	Eigenvalue	Variance explained Proportion	Cumulative
1	2.2200	0.3171	0.317
2	1.7122	0.2446	0.562
3	1.3065	0.1866	0.748
4	0.8286	0.1184	0.867
5	0.6164	0.0881	0.955
6	0.3140	0.0449	1.000
7	0.0023	0.0003	1.000

Weights of variables by eigenvector			
	Eigenvector		
	1	2	3
Smolt age 2	-0.4753	0.4876	-0.2068
Smolt age 3	-0.1416	-0.6682	0.2185
Smolt age 4	0.5873	-0.0750	0.0577
Smolt age 5	0.5199	0.3310	-0.0104
Smolt age 6-7	0.3066	0.2668	0.2052
Prop. female	0.0704	-0.0144	-0.7669
Mean length	-0.1994	0.3595	0.5252

Table 5. Summary of principal components dimension reduction analysis for small salmon and large salmon combined characteristics.

N = 47 rivers
Variables = 10

Component	Eigenvalue	Variance explained	
		Proportion	Cumulative
1	3.816	0.382	0.382
2	2.054	0.205	0.587
3	1.386	0.139	0.726
4	0.931	0.093	0.819
5	0.752	0.075	0.894
6	0.402	0.040	0.934
7	0.314	0.031	0.966

Weights of variables by eigenvector			
	Eigenvector		
	1	2	3
Smolt age 2	-0.353	-0.197	0.485
Smolt age 3	0.105	-0.429	-0.602
Smolt age 4	0.344	0.403	-0.122
Smolt age 5	0.096	0.596	0.139
Prop. female small	0.447	-0.140	0.270
Prop. female large	0.155	-0.237	0.292
Mean length small	-0.339	-0.003	0.246
Mean length large	-0.416	0.172	-0.015
Prop. returns small	0.425	0.072	0.274
Prop. maiden	-0.211	0.385	-0.273

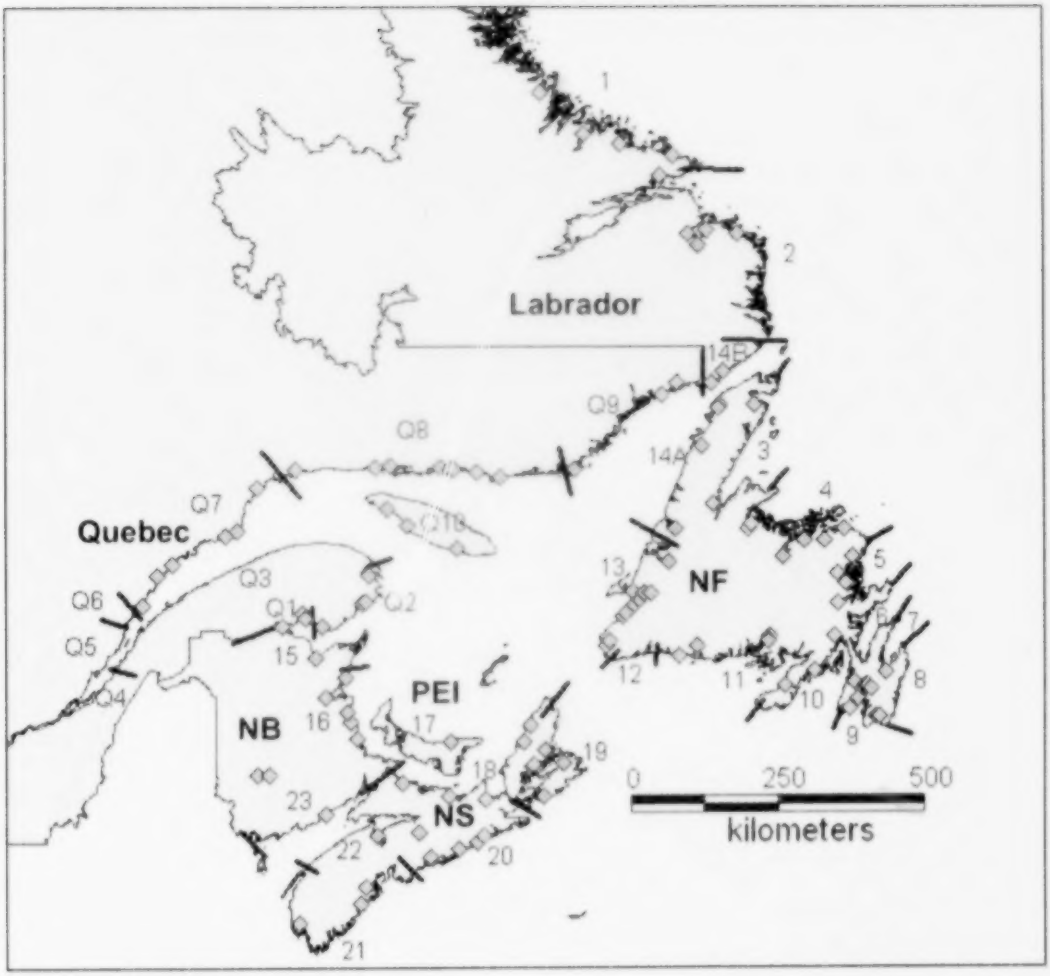

Figure 1. Map of eastern Canada showing boundaries for salmon fishing areas (SFA) and fishing zones (Q) and location of 112 rivers with biological characteristics information examined in this study. Approximate south to north orientation referenced in text and accompanying figures is the following sequence of SFAs and Qs : 23 – 22 – 21 – 20 – 19 – 18 – 17 – 16 – 15 – Q1 – Q2 – Q3 – Q7 – Q8 – Q10 – 13 – 12 – 11 – 10 – 9 – 8 – 7 – 6 – 5- 4 – 3 – 14A – Q9 – 14B – 2 -1. There are no salmon rivers sampled in zones Q3 to Q6.

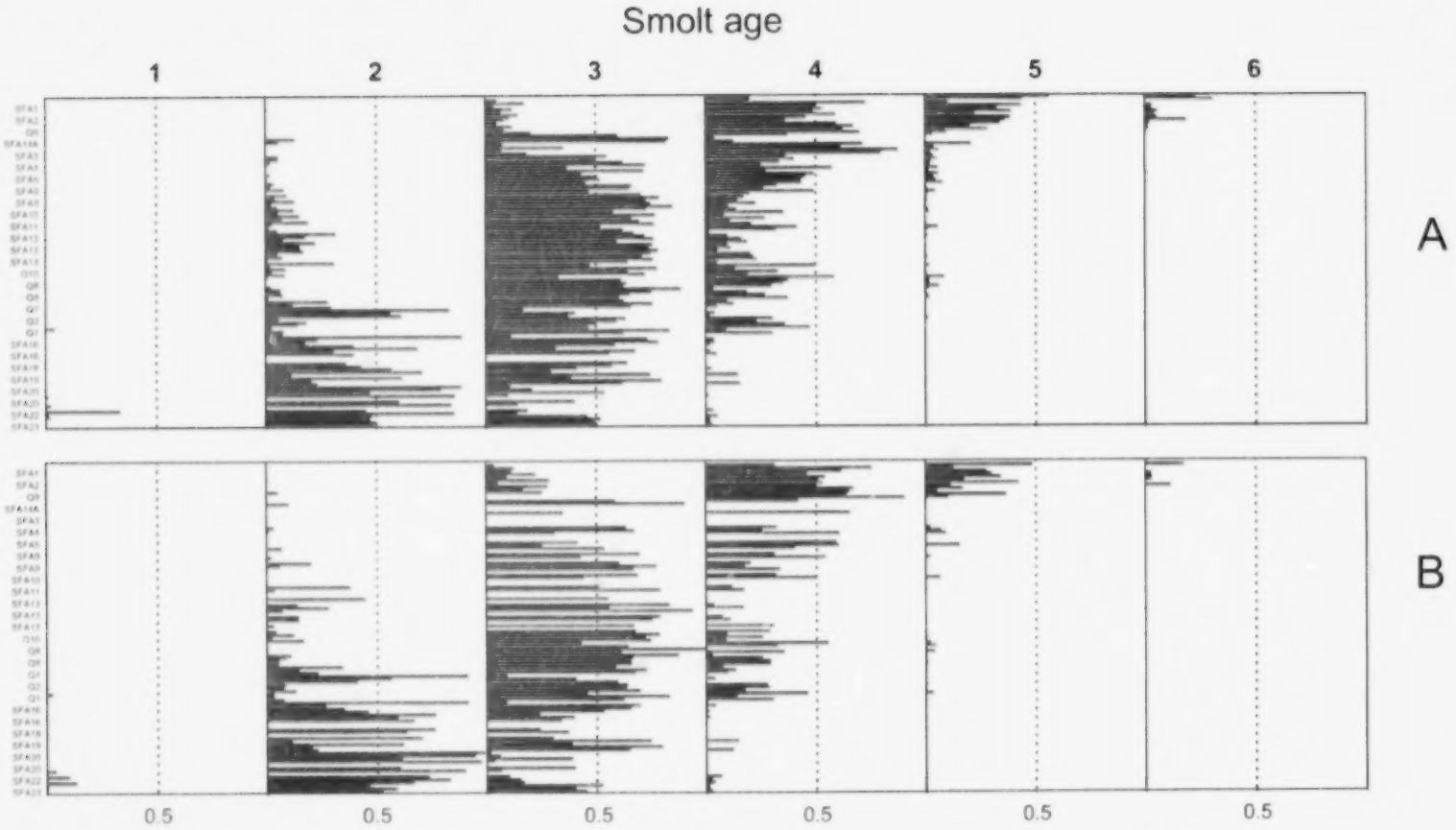

Figure 2a. Smolt age distribution (proportion at age) of large salmon (A) and small salmon (B) from sampled rivers in eastern Canada. A total of 108 rivers are represented for small salmon, 87 rivers for large salmon. River specific data are aligned in an approximate south (SFA 23) to north (SFA 1) orientation.

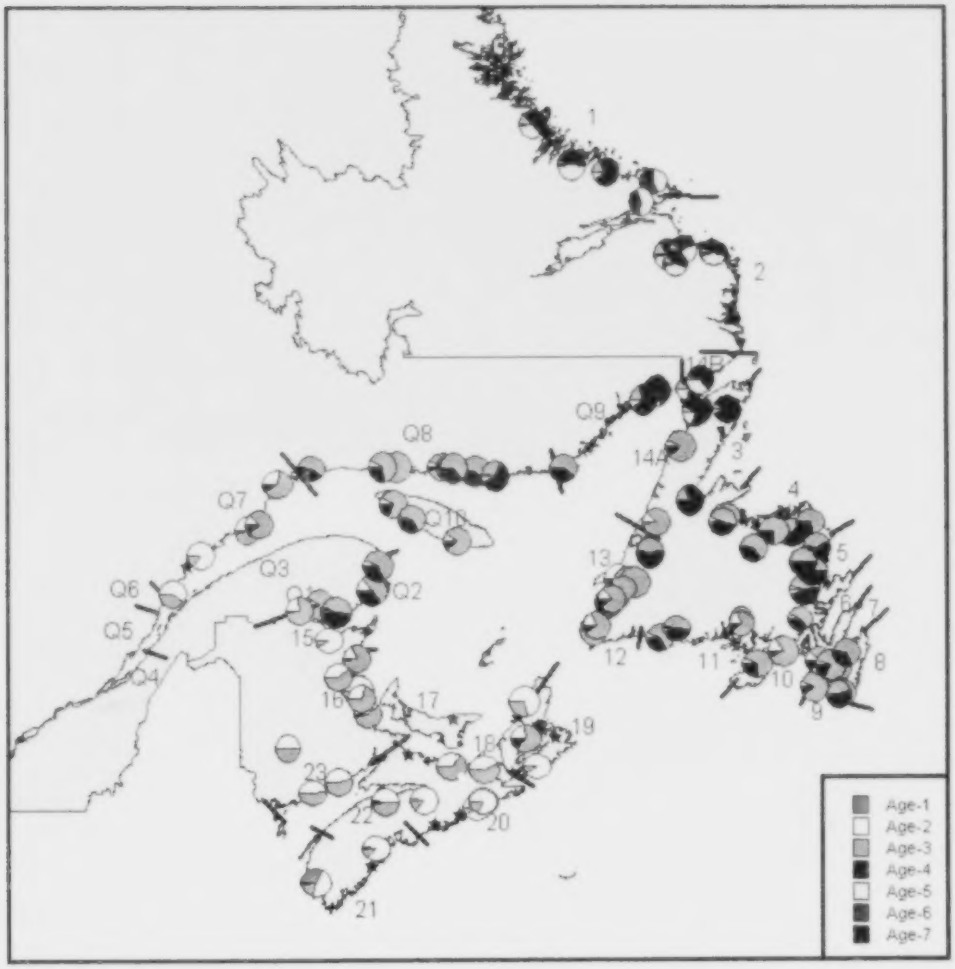

Figure 2b. Proportions at smolt age by river for small salmon from sampled rivers in eastern Canada. A total of 108 rivers are represented for small salmon.

Figure 3. Mean age (years) at smoltification (upper map) and relationship between mean age at smoltification and latitude and longitude (lower graph) from sampled rivers of eastern Canada. In the lower graph, the relative diameter of the bubble corresponds to the longitude range of the rivers (minimum = 53.16°W and maximum = 69.41°W).

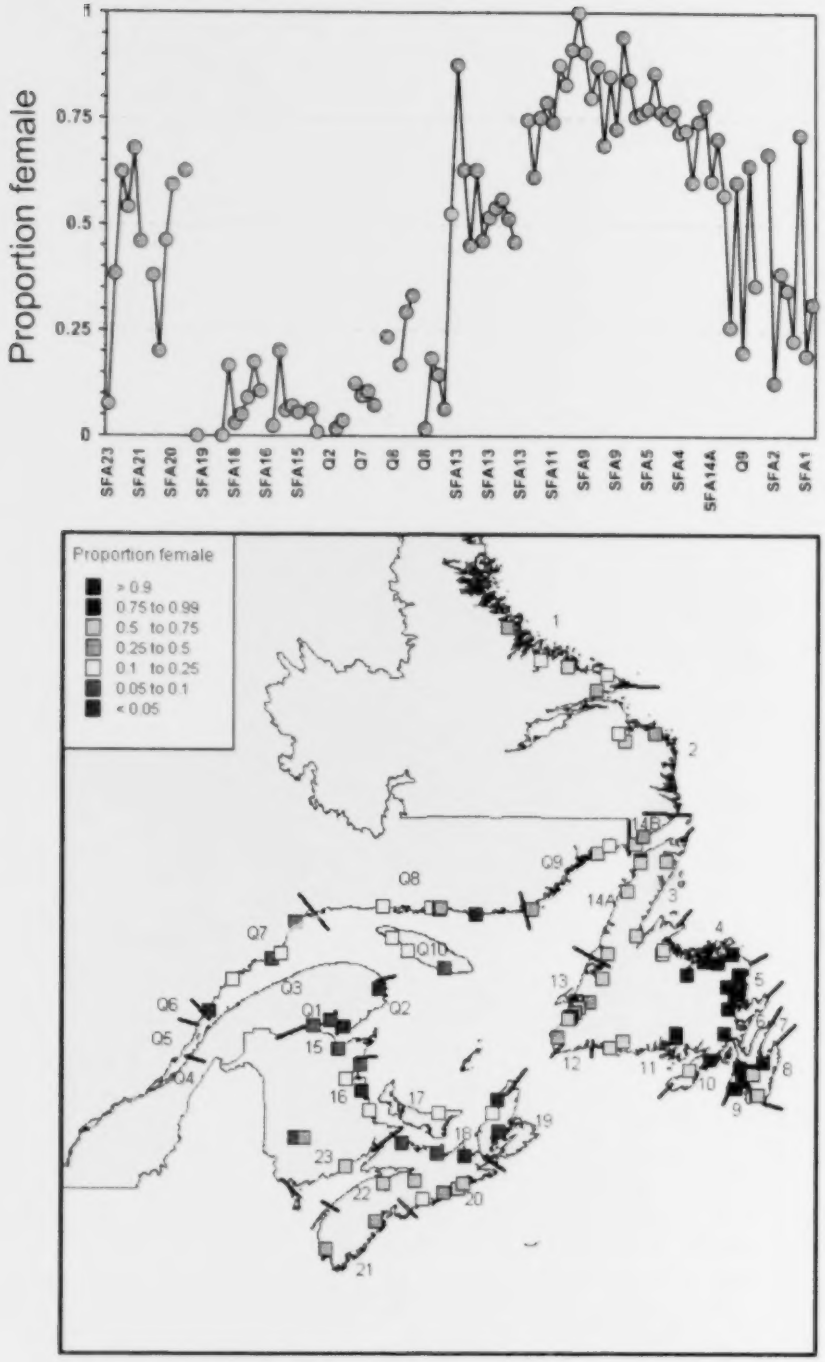

Figure 4a. The proportion female in small salmon from sampled rivers in eastern Canada. Rivers in the upper panel are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

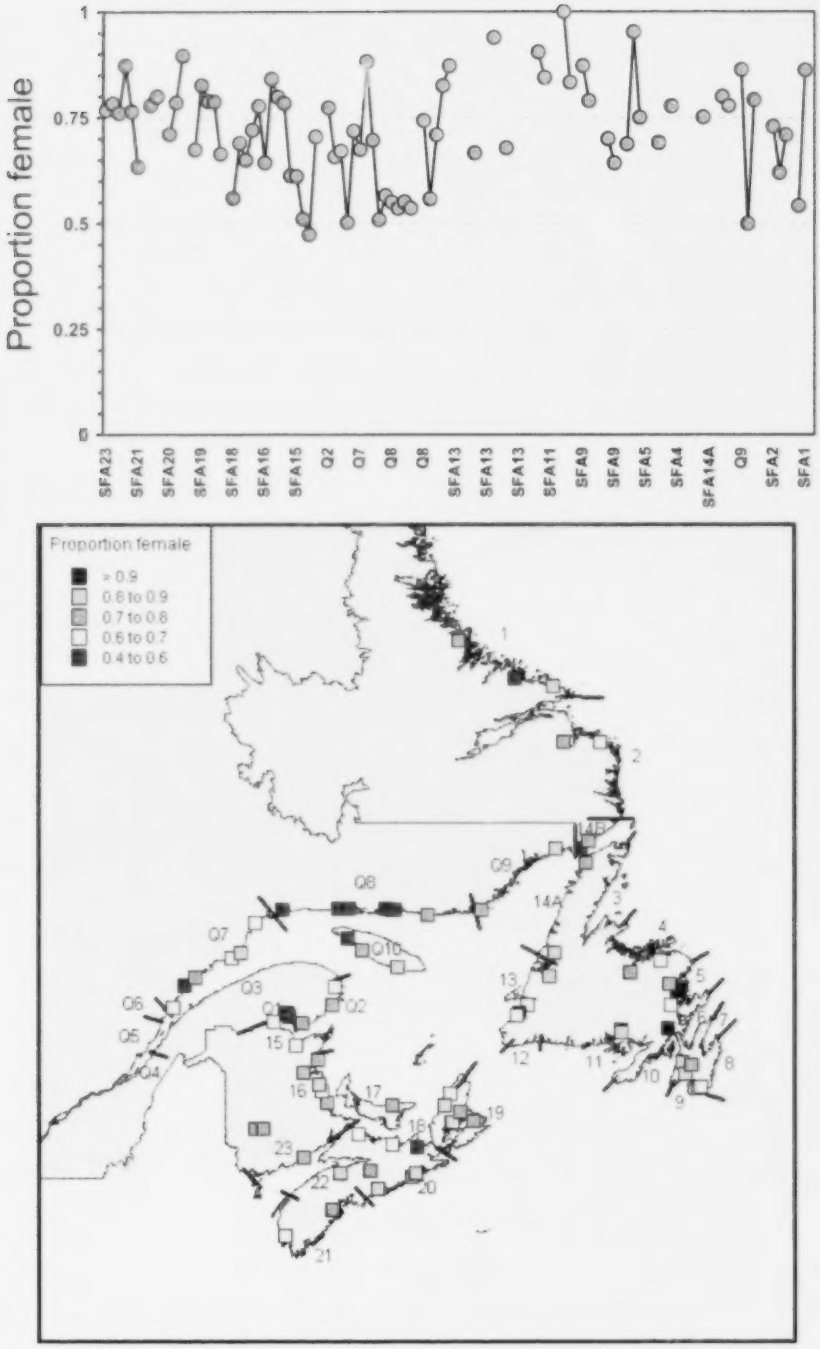

Figure 4b. The proportion female in large salmon from sampled rivers in eastern Canada. Rivers in the upper panel are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

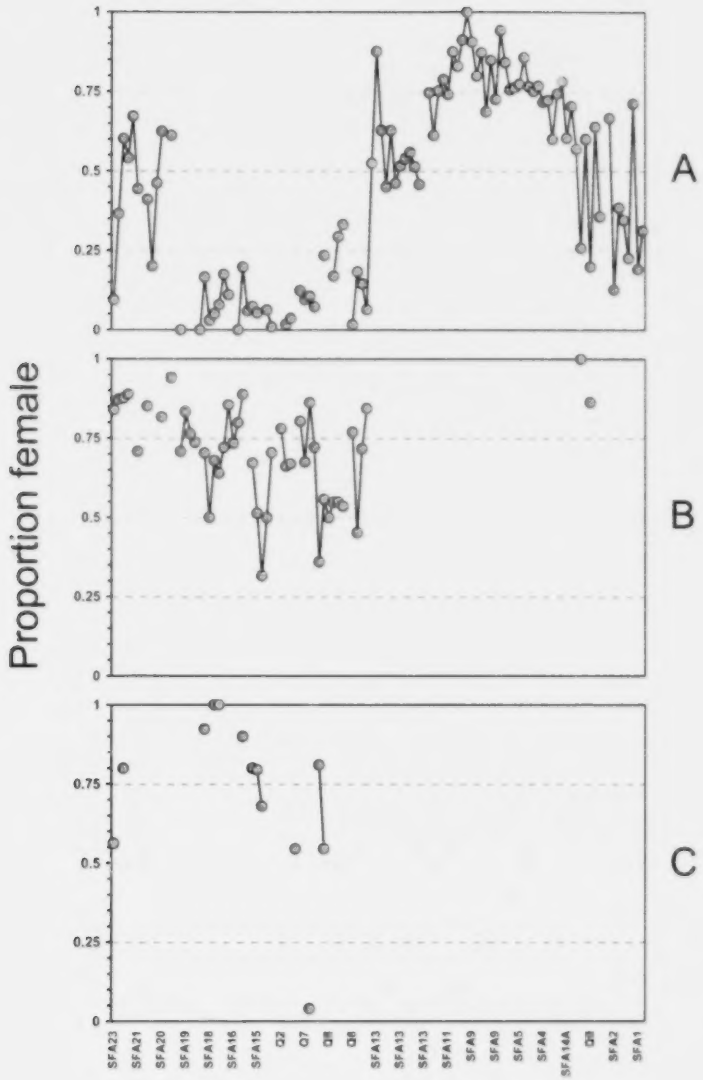

Figure 4c. The proportion female in 1SW (A), 2SW (B), and 3SW (C) maiden salmon from sampled rivers in eastern Canada. Rivers are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

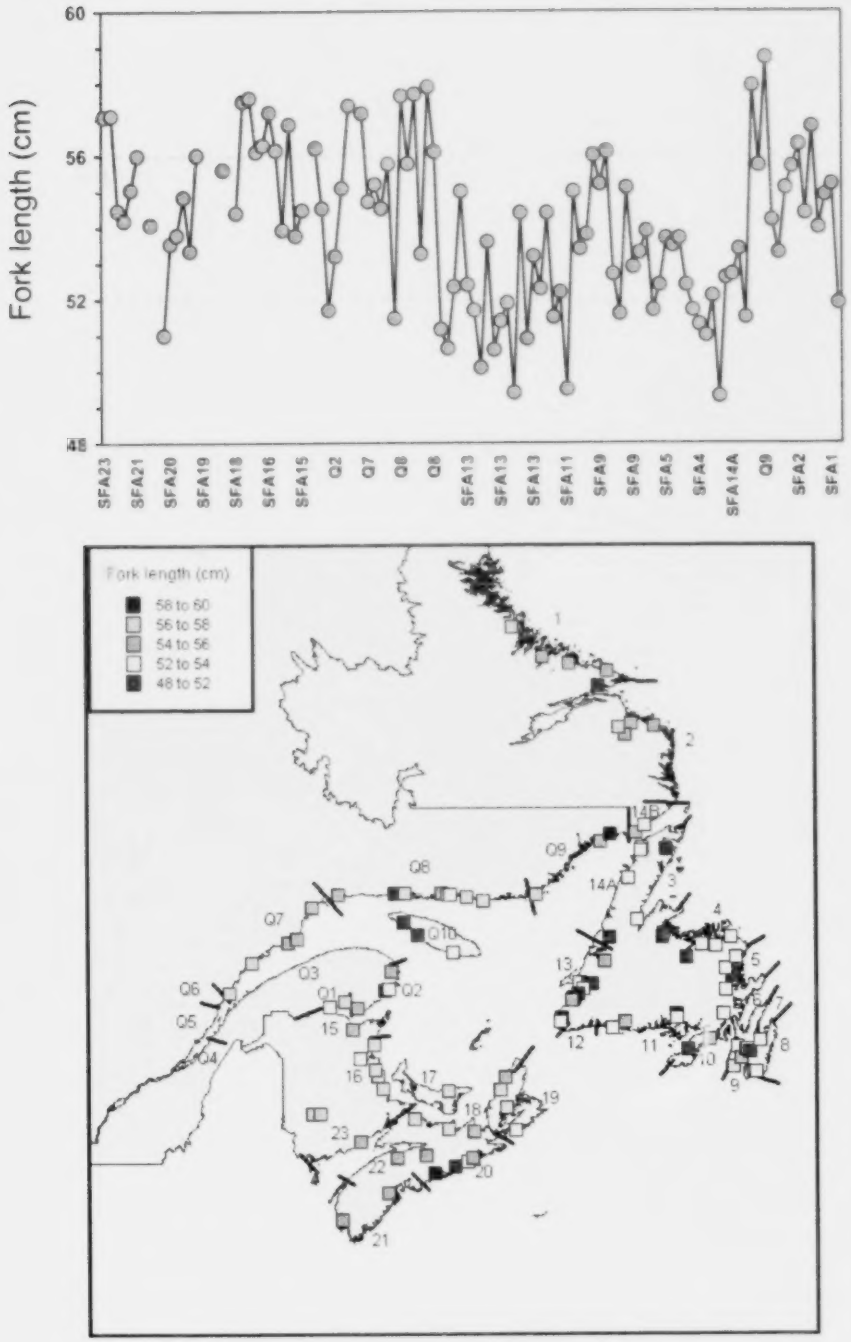

Figure 5a. Mean fork length (cm) of small salmon from sampled rivers in eastern Canada. Rivers in upper panel are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

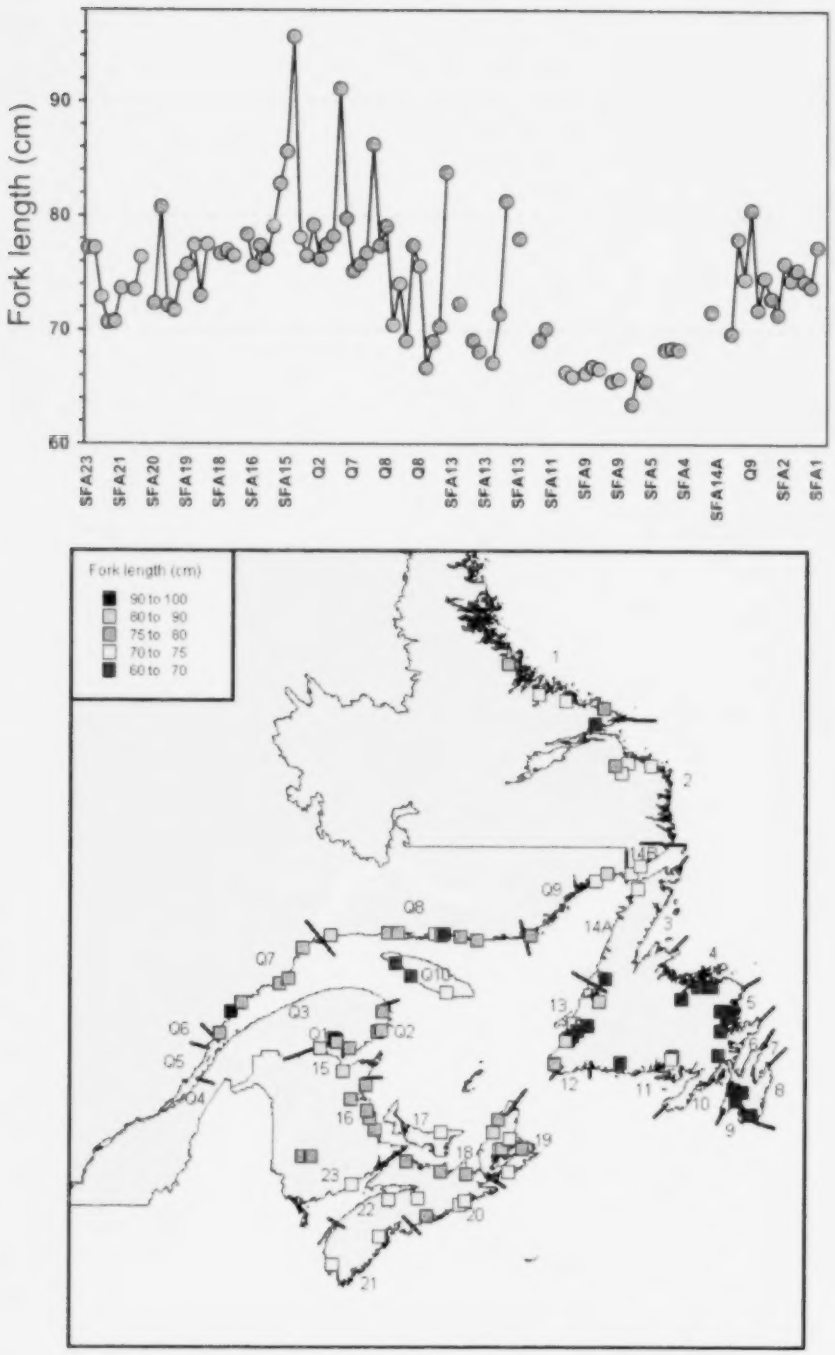

Figure 5b. Mean fork length (cm) of large salmon from sampled rivers in eastern Canada. Rivers in upper panel are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

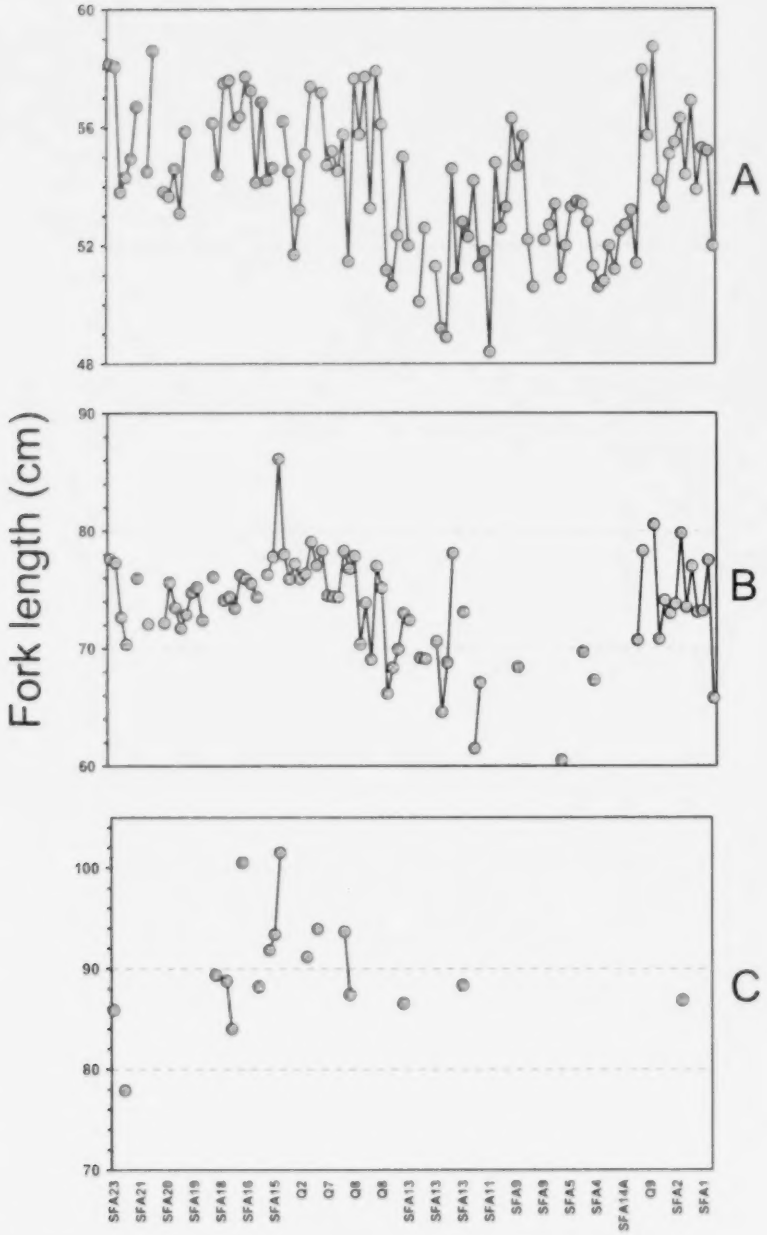

Figure 5c. Mean fork length (cm) 1SW (A), 2SW (B), and 3SW (C) maiden salmon from sampled rivers in eastern Canada. Rivers are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

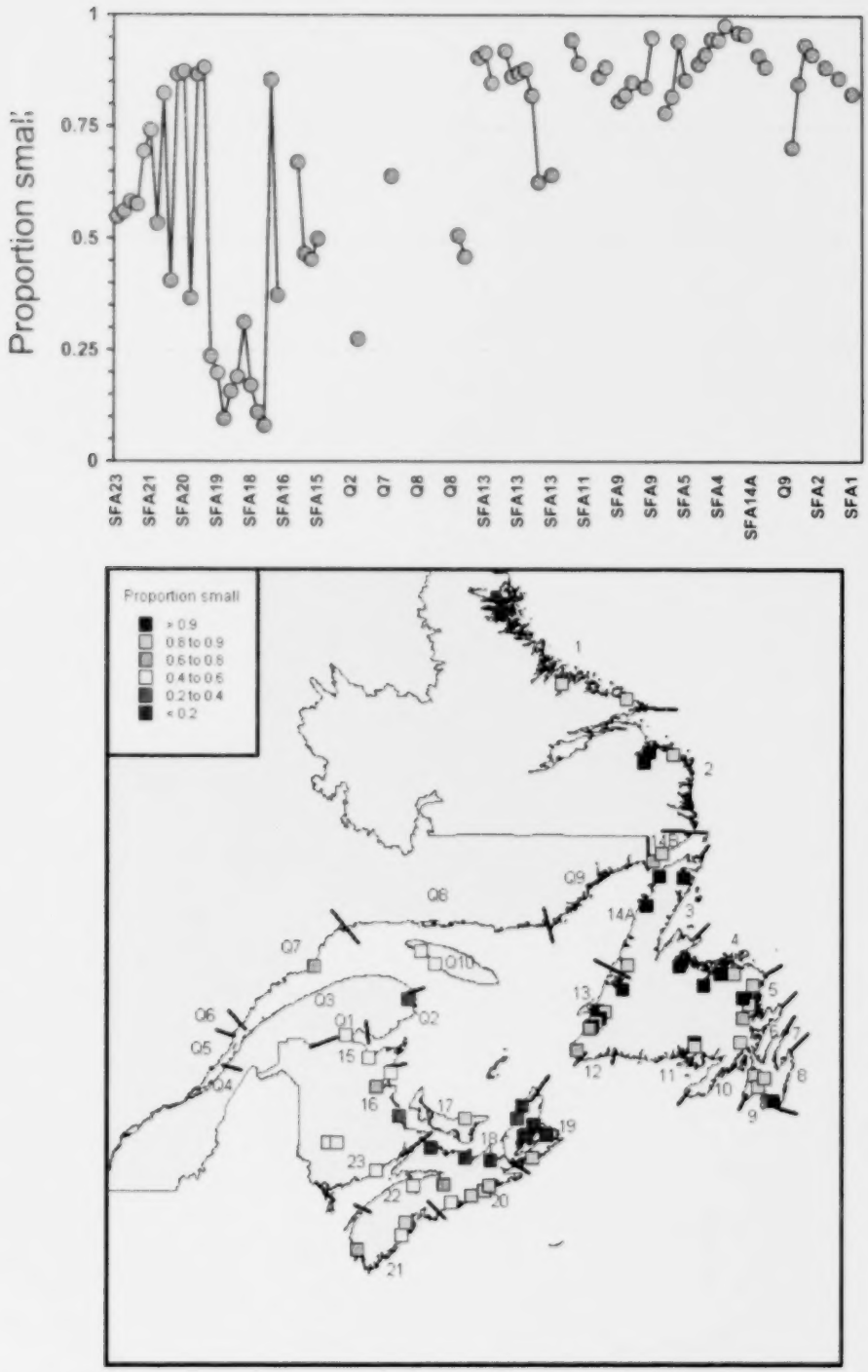

Figure 6. The proportion small salmon in the total returns to sampled rivers in eastern Canada. Rivers are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

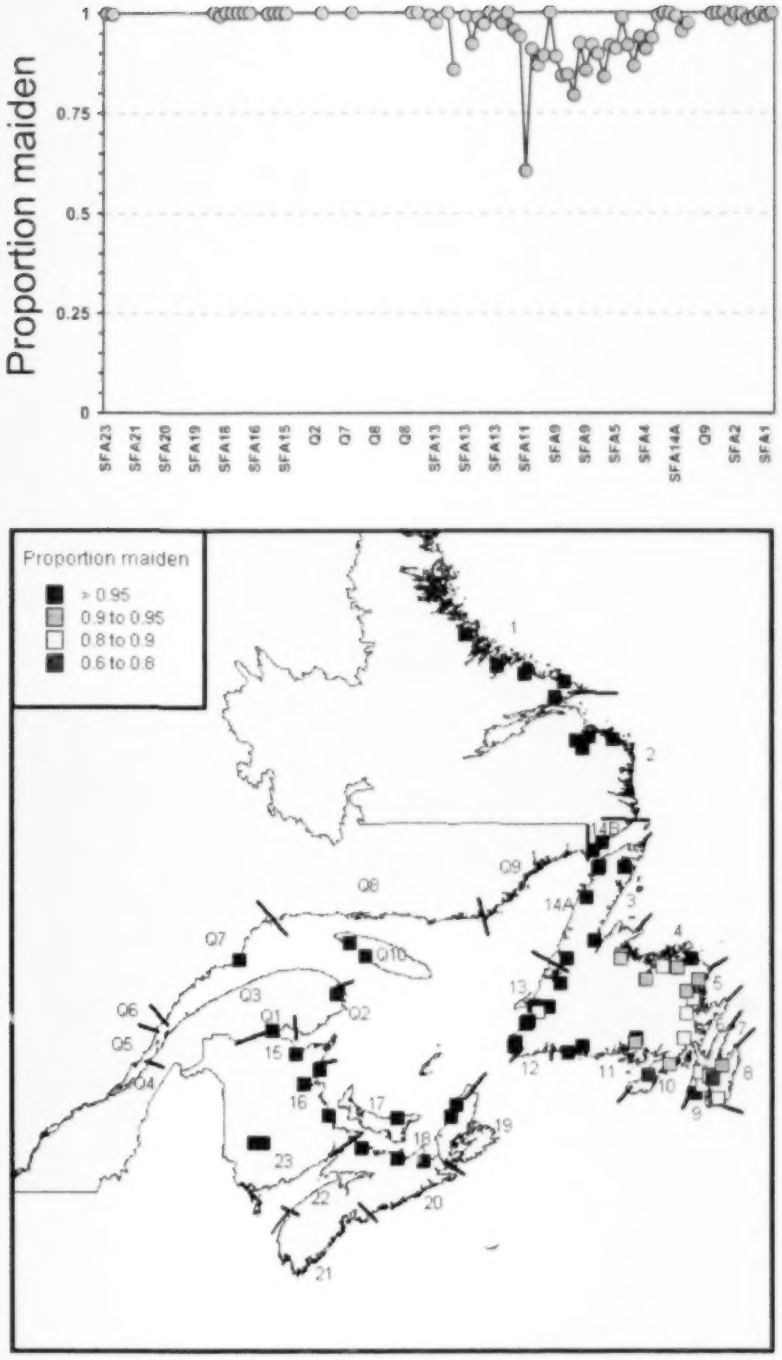

Figure 7a. Proportions of maiden salmon in the small salmon returns to sampled rivers in eastern Canada. Rivers in upper panel are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

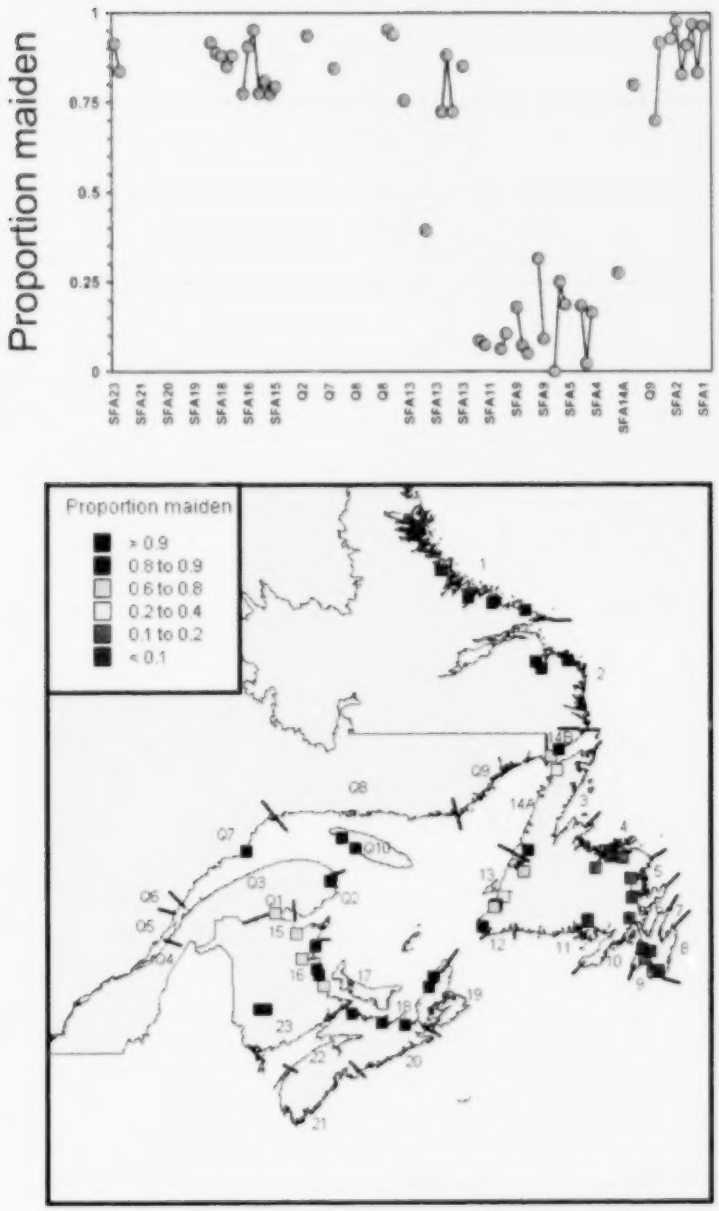

Figure 7b. Proportions of maiden salmon in the large salmon returns to sampled rivers in eastern Canada. Rivers in upper panel are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

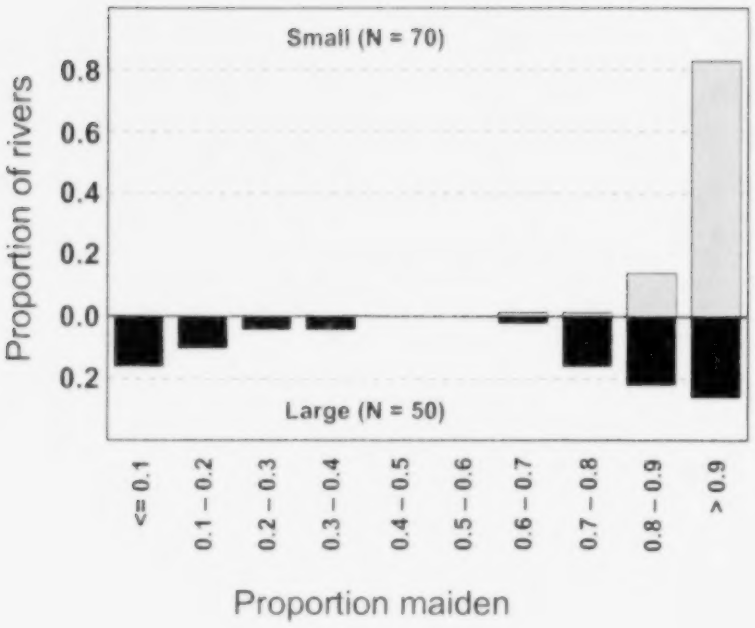

Figure 7c. Proportion of rivers based on the proportion maiden salmon in the small versus large salmon categories

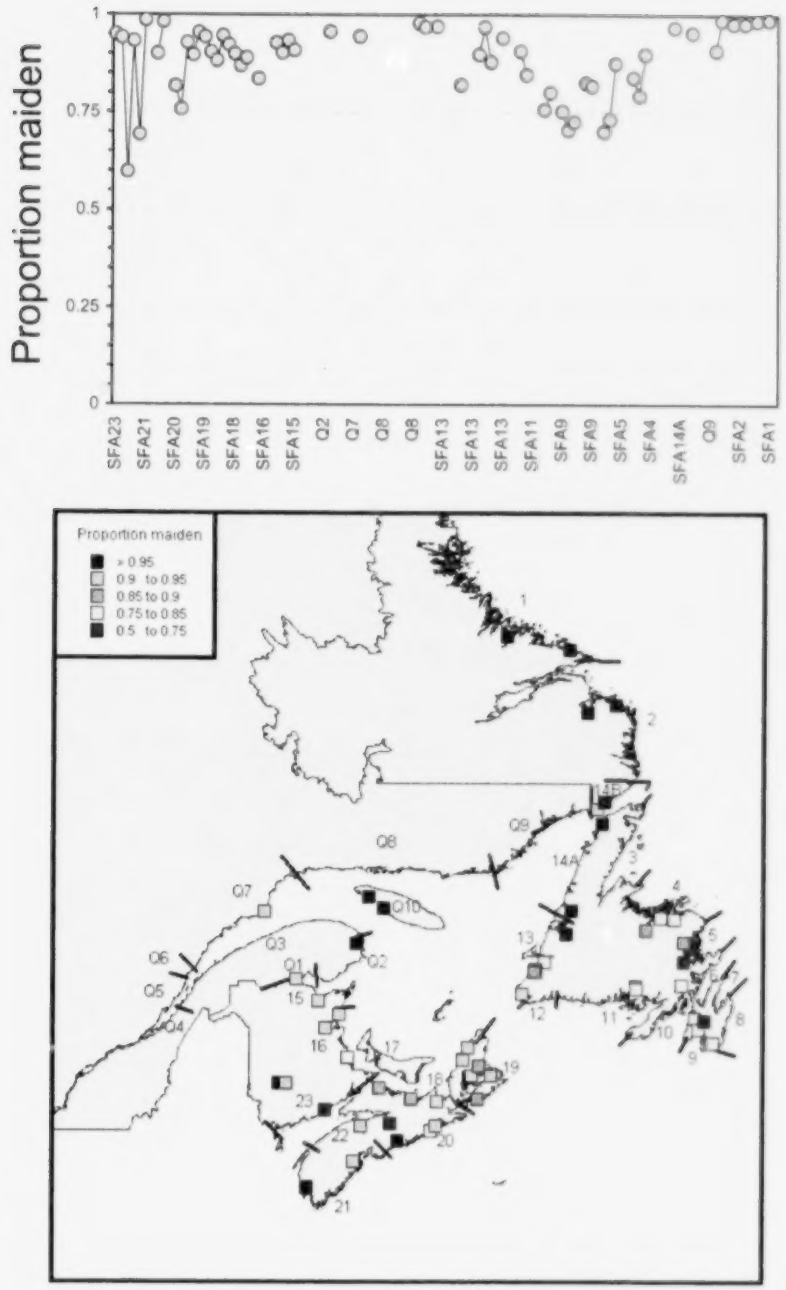

Figure 7d. Proportions of maiden salmon in the total returns to sampled rivers in eastern Canada. Rivers in upper panel are arranged in an approximate south (SFA 23) to north (SFA 1) orientation.

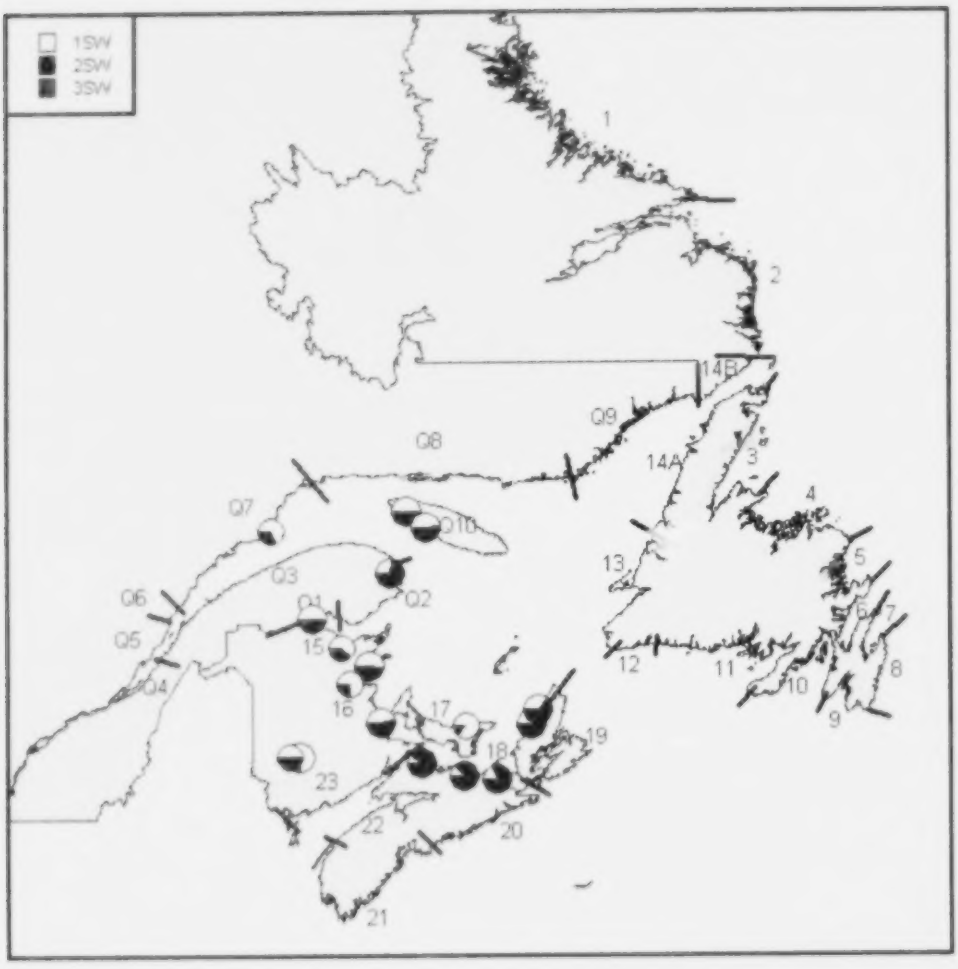

Figure 8. Proportion by maiden sea age of returns to rivers.

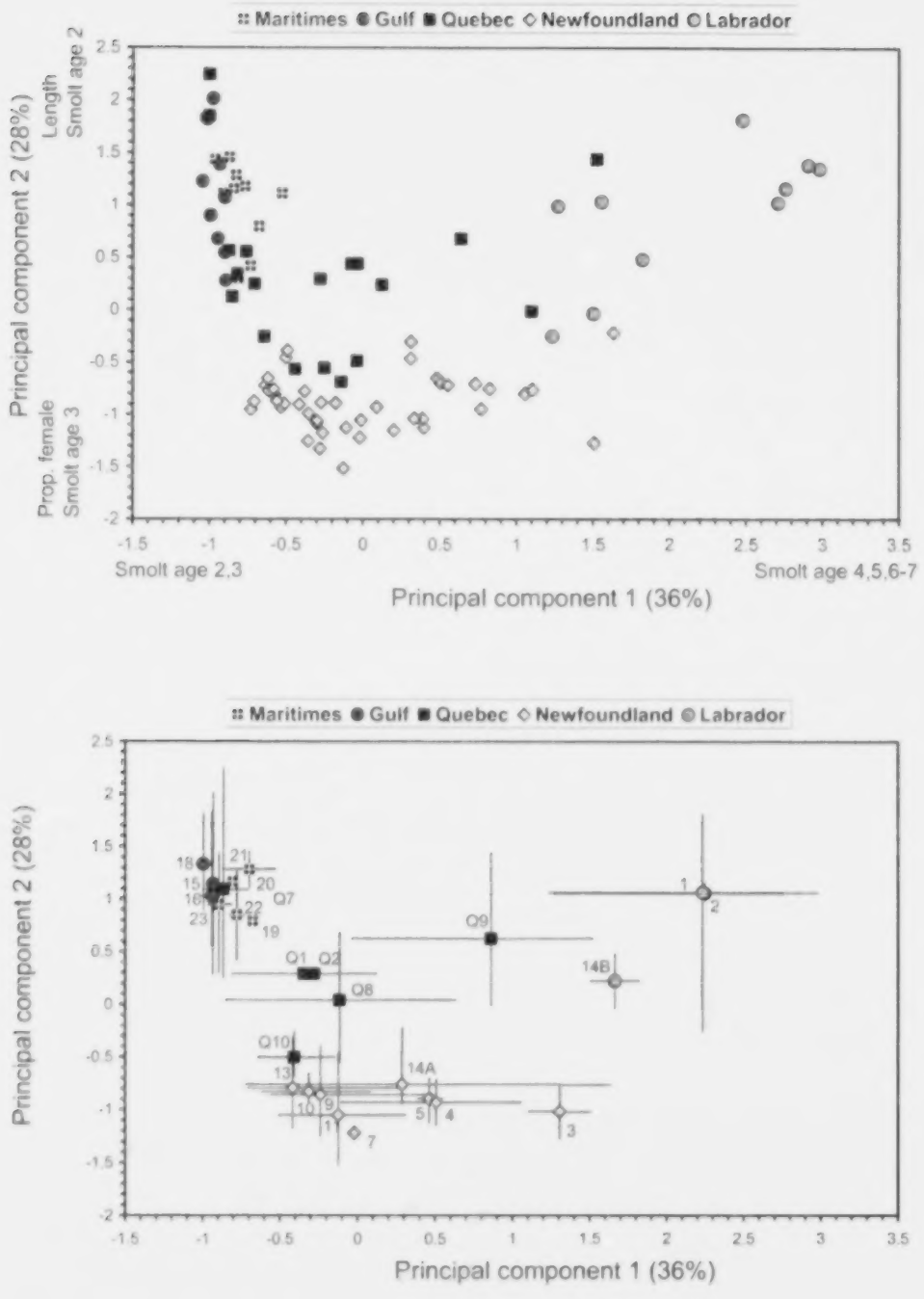
:: Maritimes ● Gulf ■ Quebec ◇ Newfoundland ○ Labrador
Principal component 2 (28%)
Length
Smolt age 2
Prop. female
Smolt age 3
Smolt age 2,3
Smolt age 4,5,6-7
Principal component 1 (36%)
:: Maritimes ● Gulf ■ Quebec ◇ Newfoundland ◎ Labrador
Principal component 2 (28%)
Principal component 1 (36%)

Figure 9. Location of 92 rivers (upper panel) and centroids of the rivers by SFA/Zone (lower) on the first and second principal components for small salmon characteristics. Error bars in the lower figure represent minimum tc maximum ranges for rivers within the SFA/Zone.

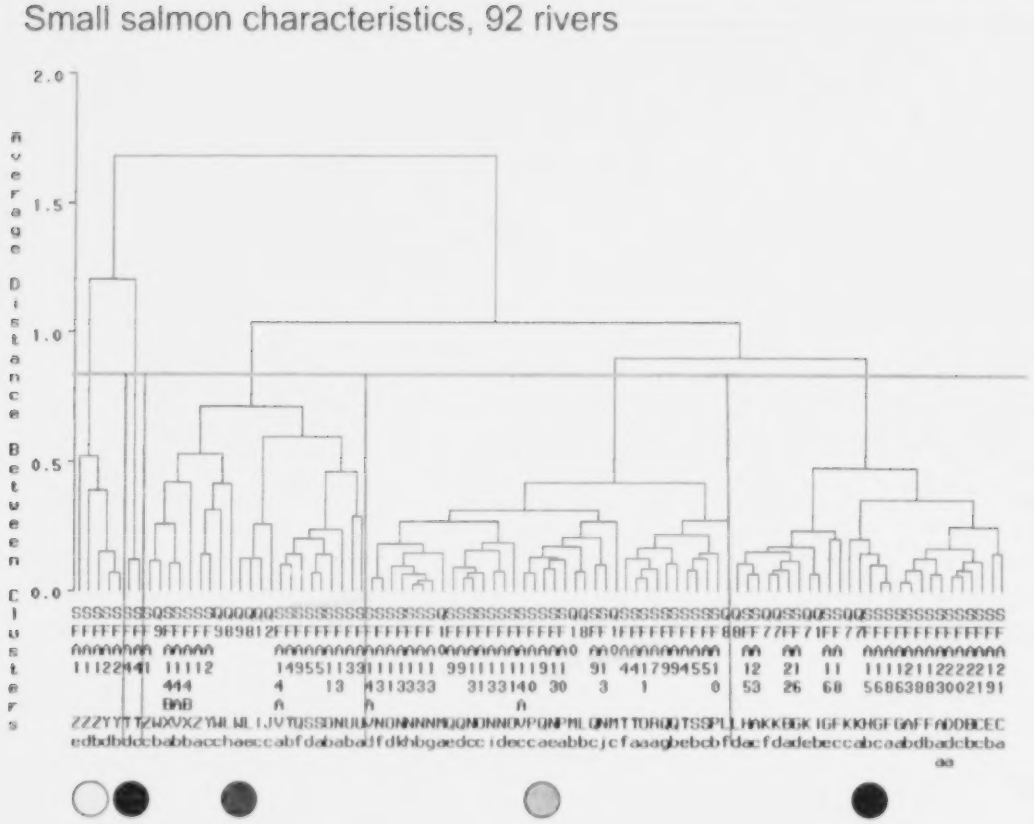

Figure 10a. Tree diagram of clustering sequence for 92 rivers based on small salmon characteristics. Coloured bullets are used to represent the rivers geographically in Figure 10b. Individual rivers can be identified by river abbreviations summarized in Appendix 1.

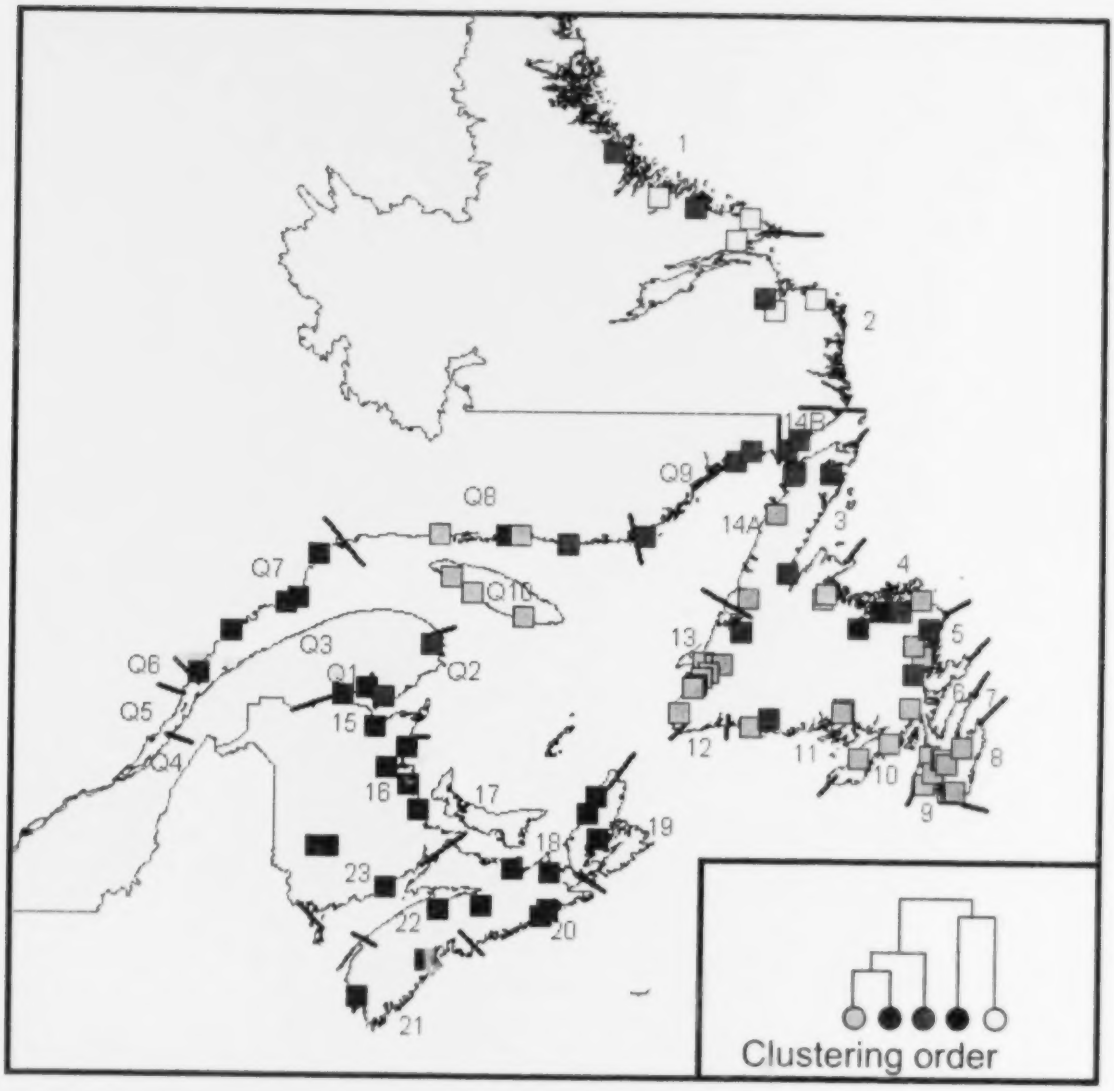

Figure 10b. Geographic distribution of river clusters as defined in Figure 10a based on small salmon characteristics.

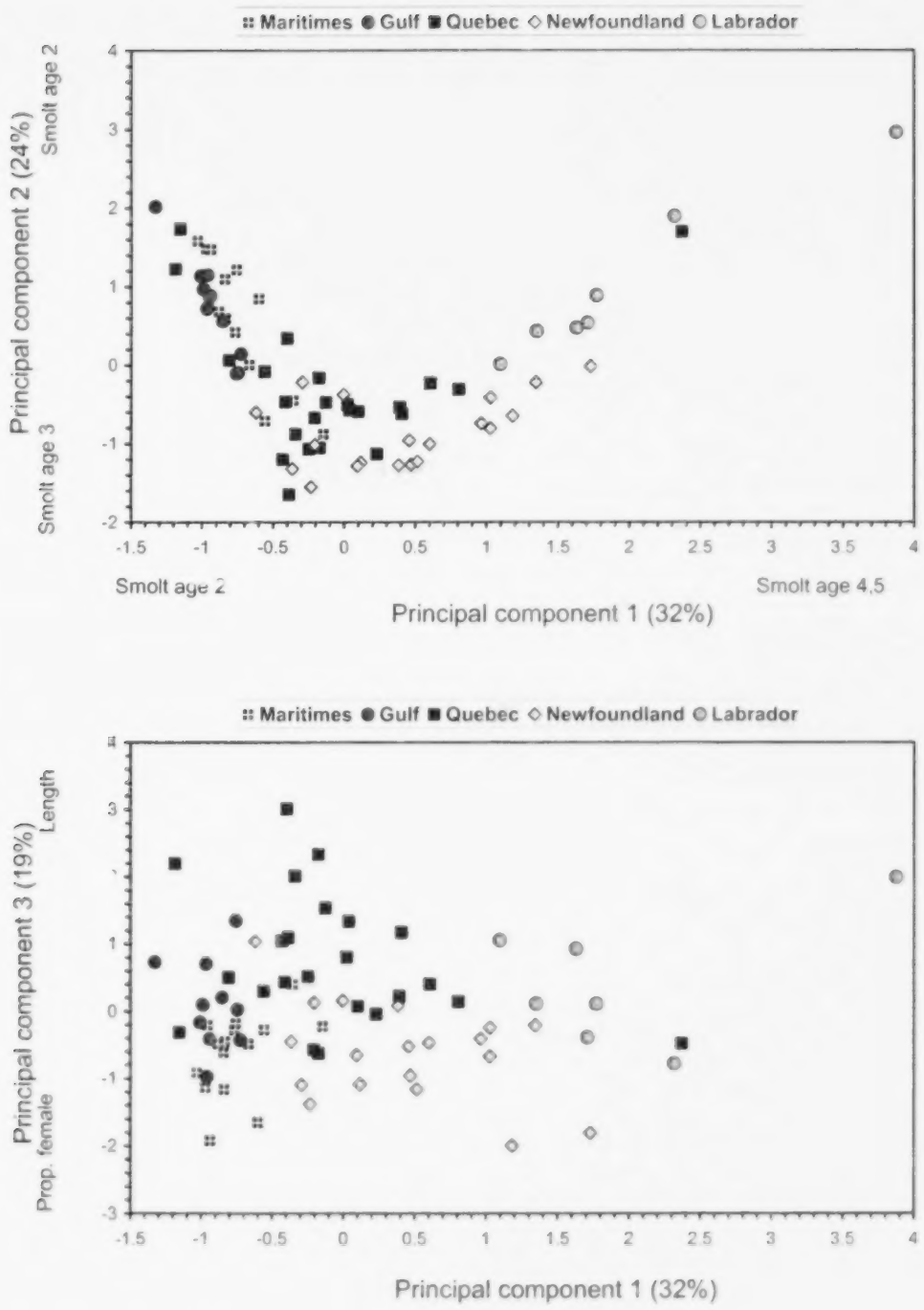

Figure 11a. Location of 74 rivers on the first and second (upper panel) and the first and third (lower) principal components for large salmon characteristics.

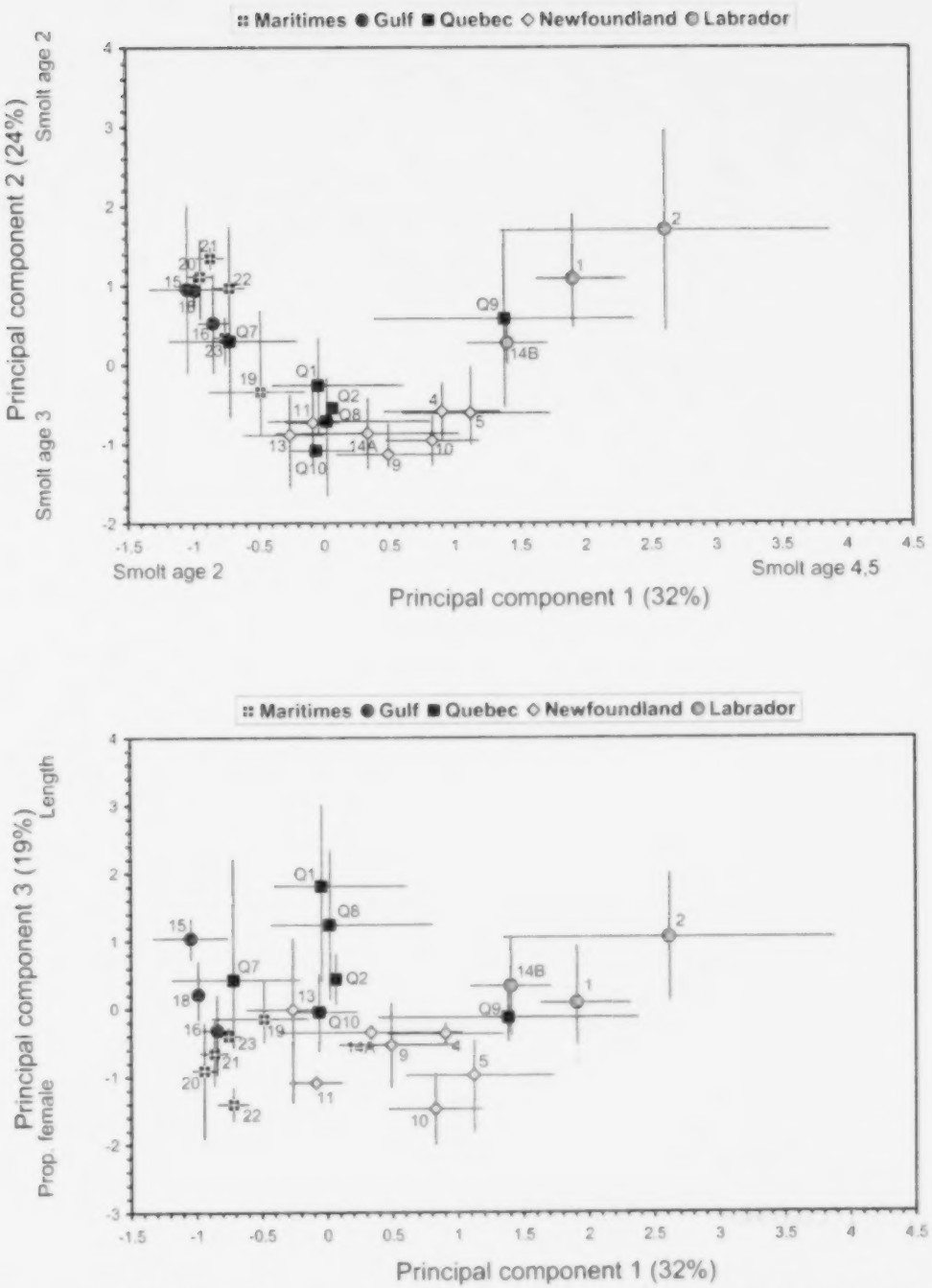
:: Maritimes ● Gulf ■ Quebec ◇ Newfoundland ◎ Labrador
Principal component 2 (24%)
Smolt age 2
Smolt age 3
Smolt age 2
Smolt age 4,5
Principal component 1 (32%)
:: Maritimes ● Gulf ■ Quebec ◇ Newfoundland ◎ Labrador
Principal component 3 (19%)
Length
Prop. female
Principal component 1 (32%)

Figure 11b. Location of centroids of the rivers by SFA/Zone on the first and second principal components (upper) and the first and third principal components (lower) for large salmon characteristics. Error bars represent minimum to maximum ranges for rivers within the SFA/Zone.

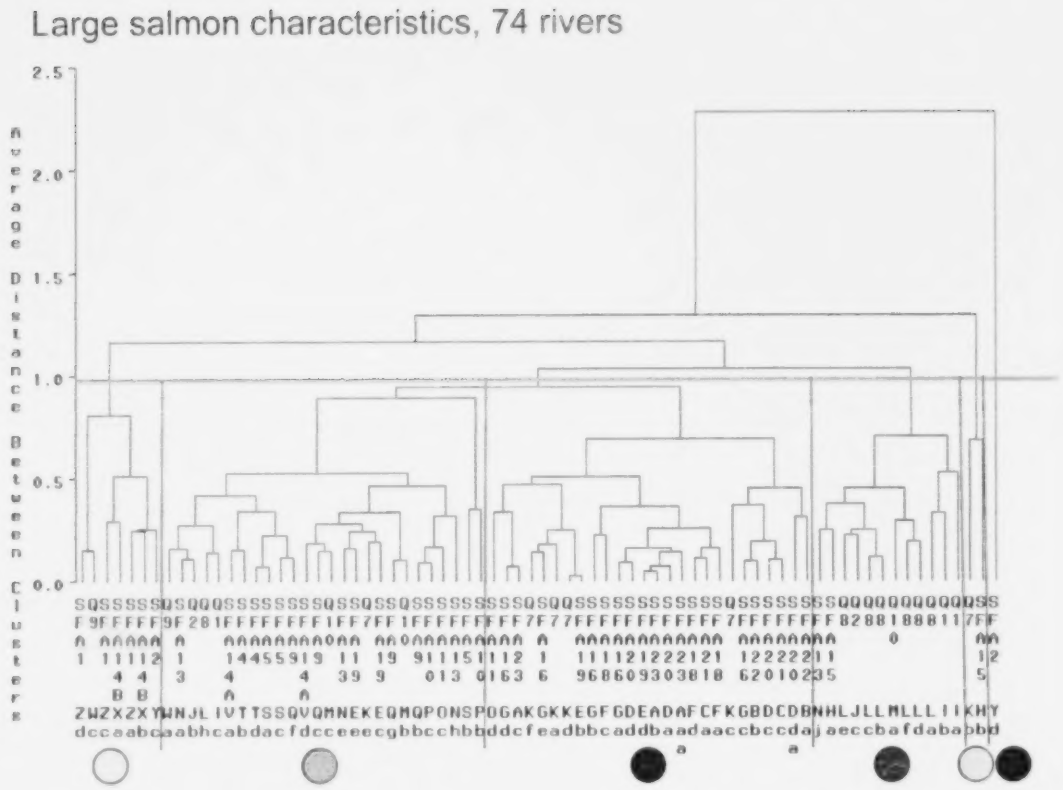

Figure 12a. Tree diagram of clustering sequence for 74 rivers based on large salmon characteristics. Coloured bullets are used to represent the rivers geographically in Figure 12b. Individual rivers can be identified by river abbreviations summarized in Appendix 2.

Figure 12b. Geographic distribution of river clusters as defined in Figure 12a based on large salmon characteristics.

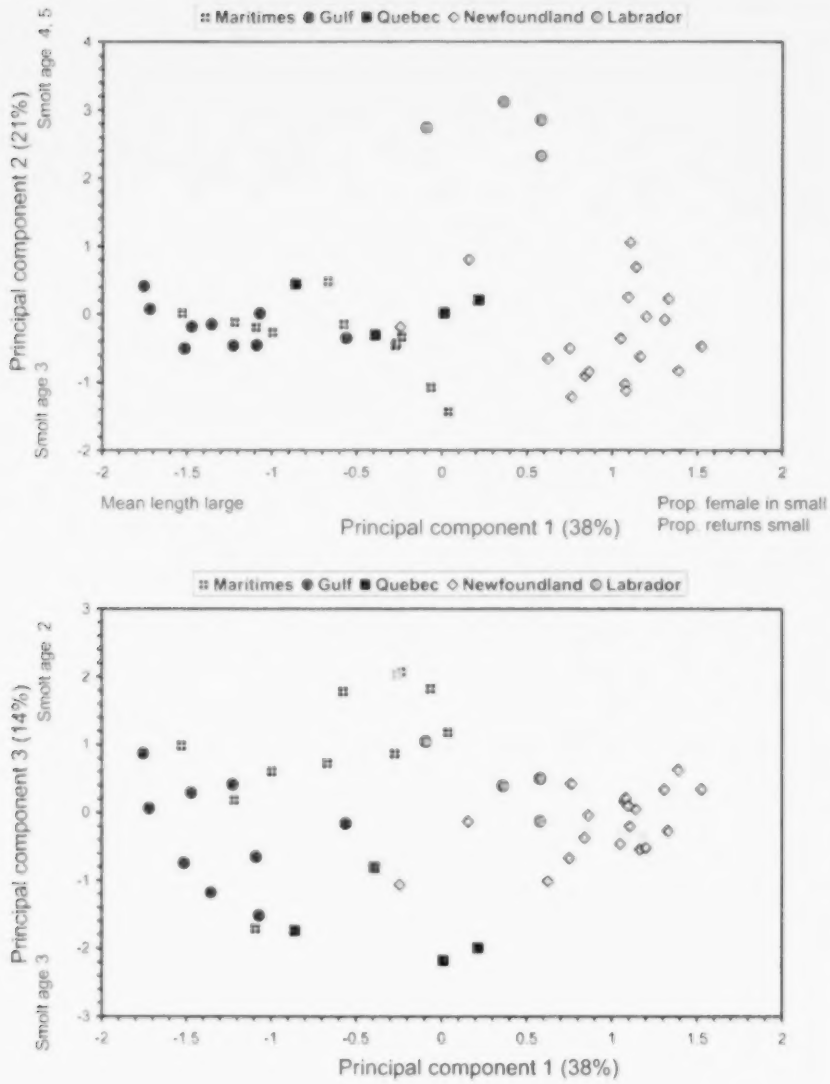

Figure 13a. Location of 47 rivers on the first and second (upper panel) and the first and third (lower) principal components for small and large salmon characteristics combined.

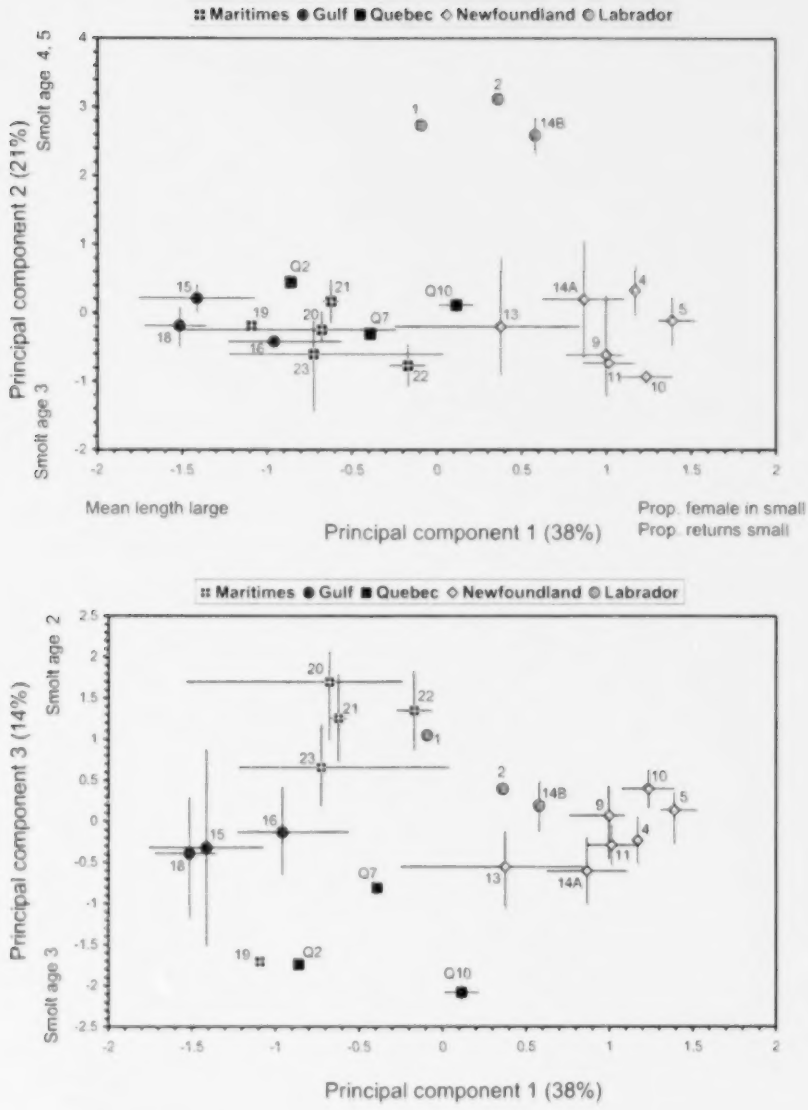

Figure 13b. Location of centroids of the 47 rivers by SFA/Zone on the first and second principal components (upper) and the first and third principal components (lower) for small and large salmon characteristics. Error bars represent minimum to maximum ranges for rivers within the SFA/Zone.

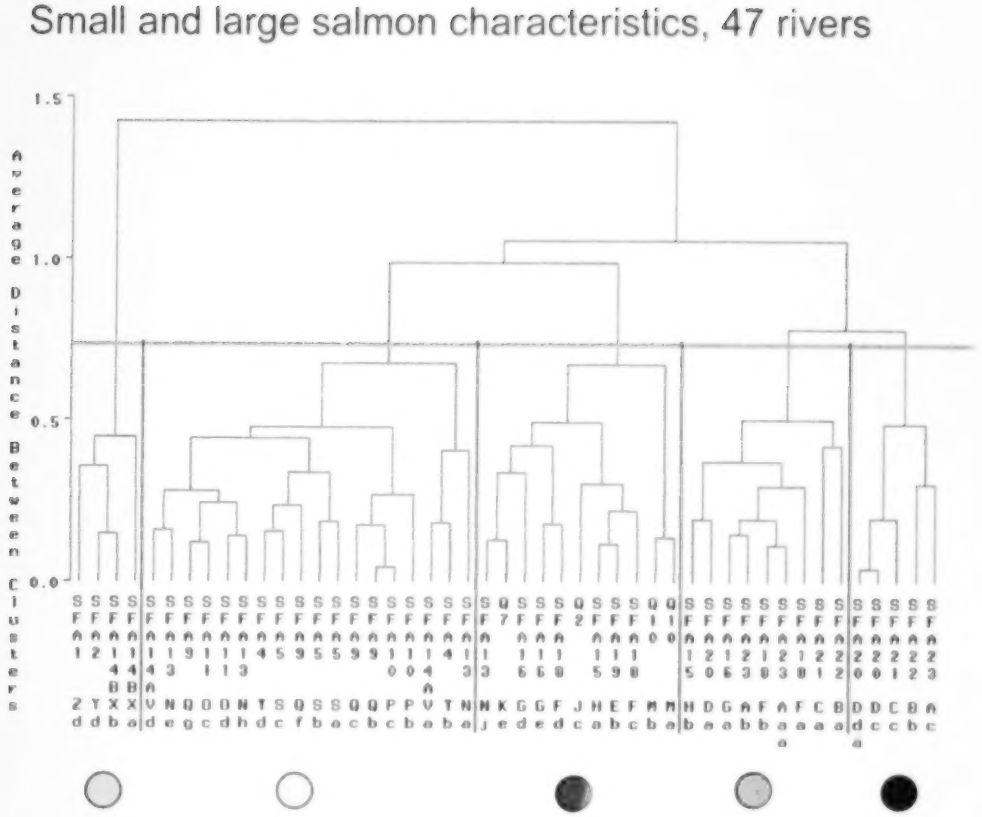

Figure 14a. Tree diagram of clustering sequence for 47 rivers based on small and large salmon characteristics. Coloured bullets are used to represent the rivers geographically in Figure 14b. Individual rivers can be identified by river abbreviations summarized in Appendix 3.

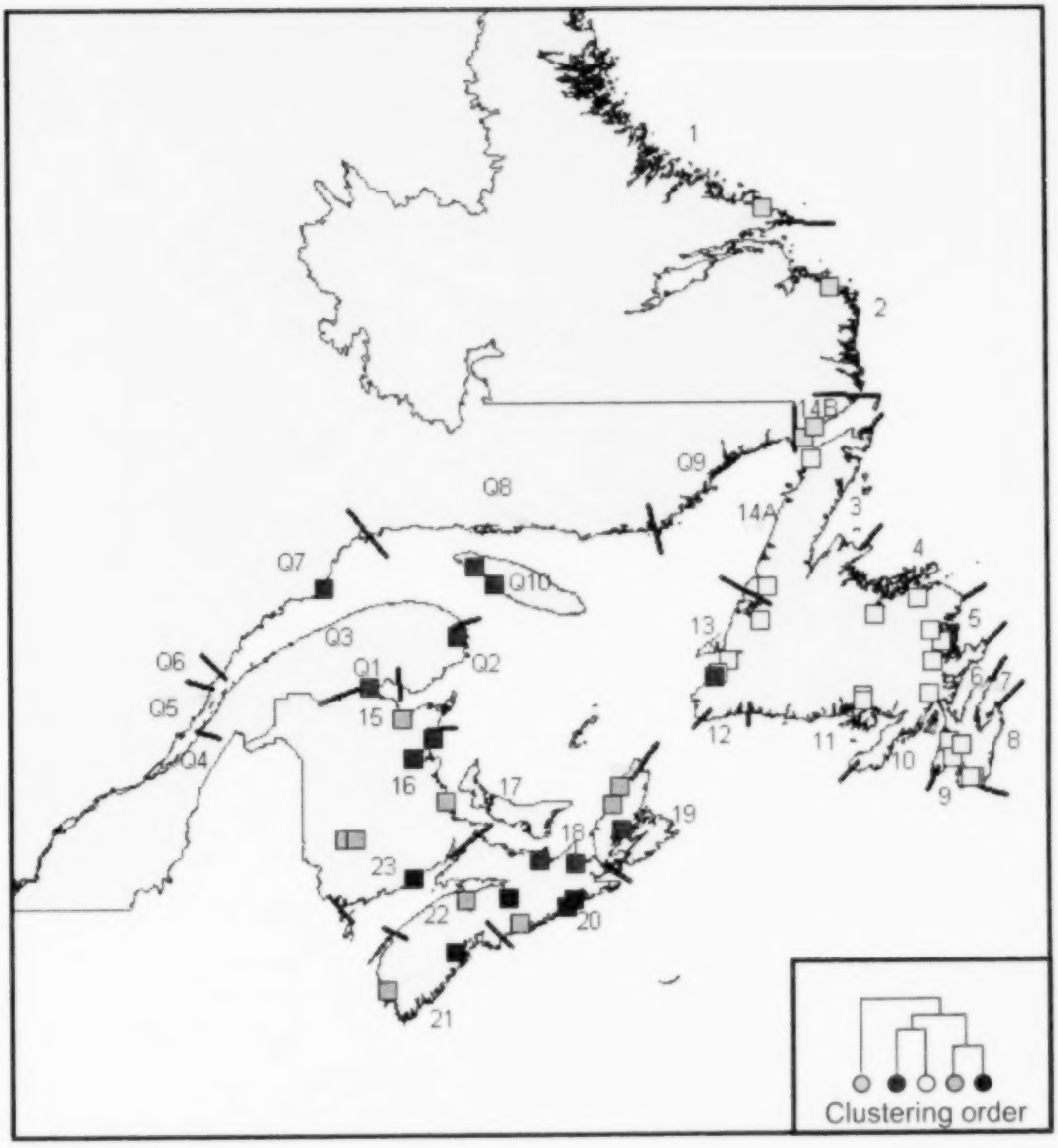

Figure 14b. Geographic distribution of river clusters as defined in Figure 14a based on small and large salmon characteristics.

Appendix 1. Biological characteristics by rivers analyzed in the small salmon grouping.

Geography	Region	Zone	River	Proportion at smolt age 2	3	4	5	Presence age 6-7	Prop female	Mean length
Aaa	Maritime	SFA23	Mactaquac-W	0.481	0.492	0.026	0.000	0	0.076	57.1
Ab	Maritime	SFA23	Nashwaak-W	0.497	0.485	0.018	0.000	0	0.383	57.1
Ac	Maritime	SFA23	Big Salmon	0.466	0.518	0.016	0.000	0	0.624	54.5
Ba	Maritime	SFA22	GASPEREAU	0.478	0.456	0.050	0.000	0	0.540	54.2
Bb	Maritime	SFA22	STEWIACKE	0.852	0.139	0.000	0.000	0	0.679	55.0
Ca	Maritime	SFA21	TUSKET	0.450	0.186	0.031	0.000	0	0.459	56.0
Cc	Maritime	SFA21	LAHAVE	0.838	0.142	0.001	0.000	0	0.379	54.1
Dc	Maritime	SFA20	LISCOMB	0.854	0.097	0.011	0.000	0	0.593	53.5
Dda	Maritime	SFA20	WEST RIVER ST MARYS	0.790	0.206	0.000	0.000	0	0.626	54.8
Eb	Maritime	SFA19	MIDDLE	0.231	0.615	0.154	0.000	0	0.000	56.0
Fa	Gulf	SFA18	Cheticamp	0.706	0.294	0.000	0.000	0	0.000	55.6
Fb	Gulf	SFA18	Margaree	0.567	0.410	0.022	0.001	0	0.166	56.2
Fc	Gulf	SFA18	South	0.430	0.570	0.000	0.000	0	0.030	54.4
Fd	Gulf	SFA18	East River	0.360	0.640	0.000	0.000	0	0.050	57.5
Ga	Gulf	SFA16	Buctouche	0.397	0.556	0.047	0.000	0	0.106	56.3
Gc	Gulf	SFA16	Kouchibouguac	0.684	0.316	0.000	0.000	0	0.024	56.1
Gd	Gulf	SFA16	Miramichi	0.397	0.584	0.019	0.000	0	0.201	53.9
Ge	Gulf	SFA16	Tabusintac	0.178	0.783	0.039	0.000	0	0.060	56.9
Ha	Gulf	SFA15	Restigouche	0.233	0.732	0.035	0.001	0	0.071	53.8
Hb	Gulf	SFA15	Nepisiguit	0.887	0.112	0.000	0.000	0	0.055	54.5
Ib	Quebec	Q1	Petite rivière Cascapédia	0.078	0.832	0.090	0.000	0	0.063	56.2
Ic	Quebec	Q1	Bonaventure	0.025	0.464	0.471	0.002	0	0.010	54.5
Jc	Quebec	Q2	Saint-Jean	0.056	0.632	0.301	0.011	0	0.018	55.1
Ka	Quebec	Q7	Des Escoumins	0.612	0.372	0.017	0.000	0	0.037	57.4
Kc	Quebec	Q7	Betsamites	0.831	0.166	0.003	0.000	0	0.124	57.2
Kd	Quebec	Q7	Godbout	0.294	0.657	0.050	0.000	0	0.095	54.7
Ke	Quebec	Q7	De la Trinité	0.121	0.754	0.123	0.001	0	0.106	55.2
Kf	Quebec	Q7	Aux Rochers	0.280	0.624	0.094	0.003	0	0.073	54.5
Lb	Quebec	Q8	Saint-Jean	0.074	0.651	0.266	0.008	0	0.234	51.5
Ld	Quebec	Q8	De la Corneille	0.065	0.885	0.034	0.016	0	0.169	55.8
Le	Quebec	Q8	Watshishou	0.021	0.624	0.296	0.059	0	0.293	57.7
Lf	Quebec	Q8	Petite rivière Watshishou	0.000	0.635	0.348	0.017	0	0.332	53.3
Lh	Quebec	Q8	Natashquan	0.008	0.328	0.580	0.084	0	0.017	56.1
Ma	Quebec	Q10	Bec-Scie	0.084	0.719	0.191	0.006	0	0.183	51.2
Mb	Quebec	Q10	Jupiter	0.027	0.644	0.326	0.003	0	0.145	50.6
Mc	Quebec	Q10	De la Chaloupe	0.089	0.777	0.132	0.002	0	0.064	52.3
Na	Newfoundland	SFA13	Humber River	0.020	0.471	0.493	0.016	0	0.525	55.0
Nb	Newfoundland	SFA13	Romaines Brook	0.308	0.641	0.051	0.000	0	0.877	52.4
Nc	Newfoundland	SFA13	Harrys River	0.009	0.758	0.228	0.005	0	0.629	51.7
Nd	Newfoundland	SFA13	Southwest and Bottom Brooks	0.072	0.708	0.213	0.007	0	0.450	50.1
Ne	Newfoundland	SFA13	Flat Bay Brook	0.052	0.748	0.200	0.000	0	0.628	53.6
Nf	Newfoundland	SFA13	Fischells Brook	0.168	0.780	0.052	0.000	0	0.462	50.6
Ng	Newfoundland	SFA13	Robinsons River	0.153	0.737	0.110	0.000	0	0.516	51.4
Nh	Newfoundland	SFA13	Middle Barachois River	0.150	0.755	0.096	0.000	0	0.539	51.9
Ni	Newfoundland	SFA13	Crabbes River	0.222	0.593	0.185	0.000	0	0.559	49.4
Nj	Newfoundland	SFA13	Highlands River	0.077	0.759	0.161	0.003	0	0.514	54.4
Nk	Newfoundland	SFA13	Grand Codroy River	0.176	0.720	0.096	0.008	0	0.458	50.9
Oa	Newfoundland	SFA11	Grandy Brook	0.051	0.620	0.319	0.010	0	0.747	52.3
Ob	Newfoundland	SFA11	White Bear River	0.014	0.518	0.413	0.055	0	0.612	54.4
Oc	Newfoundland	SFA11	Conne River	0.026	0.763	0.205	0.005	0	0.752	51.5
Od	Newfoundland	SFA11	Little River	0.192	0.694	0.109	0.003	0	0.788	52.2
Oe	Newfoundland	SFA11	Garnish River	0.073	0.661	0.266	0.000	0	0.741	49.5
Pa	Newfoundland	SFA10	Cape Roger Brook	0.152	0.768	0.081	0.000	0	0.875	55.0
Pb	Newfoundland	SFA10	Pipers Hole Brook	0.054	0.577	0.354	0.015	0	0.830	53.4

Appendix 1 (continued). Biological characteristics by rivers analyzed in the small salmon grouping.

				Proportion at smolt age				Presence	Prop.	Mean
Geography	Region	Zone	River	2	3	4	5	age 6-7	female	length
Pc	Newfoundland	SFA10	Northeast River	0.126	0.726	0.136	0.012	0	0.913	53.8
Qa	Newfoundland	SFA9	Branch River	0.051	0.848	0.102	0.000	0	1.000	56.0
Qb	Newfoundland	SFA9	Little Salmonier River	0.025	0.748	0.224	0.004	0	0.906	55.2
Qc	Newfoundland	SFA9	Rocky River	0.128	0.725	0.142	0.006	0	0.799	56.1
Qd	Newfoundland	SFA9	Colinet River	0.040	0.786	0.169	0.005	0	0.872	52.7
Qe	Newfoundland	SFA9	Salmonier River	0.092	0.702	0.195	0.011	0	0.687	51.6
Qf	Newfoundland	SFA9	Northeast Brook	0.003	0.466	0.489	0.042	0	0.849	55.1
Qg	Newfoundland	SFA9	Biscay Bay River	0.081	0.653	0.259	0.007	0	0.726	52.9
Ra	Newfoundland	SFA7	North Arm River	0.020	0.660	0.320	0.000	0	0.942	53.3
Sa	Newfoundland	SFA5	Northwest River	0.036	0.451	0.432	0.076	0	0.841	53.9
Sb	Newfoundland	SFA5	Terra Nova River	0.006	0.517	0.430	0.045	0	0.755	51.7
Sc	Newfoundland	SFA5	Middle Brook	0.006	0.508	0.452	0.033	0	0.763	52.4
Sd	Newfoundland	SFA5	Indian Bay Brook	0.016	0.431	0.488	0.057	0	0.773	53.7
Ta	Newfoundland	SFA4	Ragged Harbour River	0.000	0.716	0.272	0.012	0	0.857	53.5
Tb	Newfoundland	SFA4	Gander River	0.004	0.367	0.572	0.055	0	0.766	53.7
Tc	Newfoundland	SFA4	Campbellton	0.006	0.725	0.248	0.021	1	0.751	52.4
Td	Newfoundland	SFA4	Exploits River	0.020	0.621	0.333	0.025	1	0.768	51.7
Te	Newfoundland	SFA4	Riverhead Brook	0.053	0.500	0.398	0.049	0	0.717	51.3
Tf	Newfoundland	SFA4	Indian Brook	0.054	0.548	0.363	0.033	0	0.722	51.0
Ua	Newfoundland	SFA3	Main River	0.000	0.185	0.792	0.023	0	0.600	52.1
Ub	Newfoundland	SFA3	Salmon River	0.000	0.071	0.871	0.058	0	0.743	49.3
Va	Newfoundland	SFA14A	West River (WAB)	0.001	0.350	0.611	0.036	0	0.781	52.6
Vb	Newfoundland	SFA14A	Ste. Genevieve River	0.000	0.075	0.710	0.206	0	0.604	52.7
Vc	Newfoundland	SFA14A	Torrent River	0.057	0.818	0.125	0.000	0	0.704	53.4
Vd	Newfoundland	SFA14A	Lomond River	0.131	0.830	0.039	0.000	0	0.570	51.5
Wa	Quebec	Q9	Étamamiou	0.004	0.597	0.369	0.030	0	0.258	57.9
Wb	Quebec	Q9	Du Vieux Fort	0.000	0.205	0.698	0.092	0	0.600	55.7
Wc	Quebec	Q9	Saint-Paul	0.000	0.082	0.621	0.280	0	0.199	58.7
Xa	Labrador	SFA14B	Forteau Brook	0.000	0.119	0.667	0.201	0	0.639	54.2
Xb	Labrador	SFA14B	Pinware River	0.000	0.050	0.591	0.339	0	0.357	53.3
Ya	Labrador	SFA2	Paradise River	0.004	0.103	0.453	0.384	1	0.667	55.7
Yc	Labrador	SFA2	Eagle River	0.003	0.146	0.587	0.224	0	0.126	56.3
Yd	Labrador	SFA2	Sand Hill River	0.001	0.069	0.487	0.387	1	0.385	54.4
Za	Labrador	SFA1	Hunt River	0.005	0.118	0.527	0.323	0	0.346	56.8
Zb	Labrador	SFA1	English River	0.000	0.038	0.493	0.435	1	0.226	54.0
Zc	Labrador	SFA1	Big River	0.000	0.174	0.725	0.101	0	0.712	54.9
Zd	Labrador	SFA1	Big Brook (Michaels River)	0.000	0.050	0.199	0.440	1	0.191	55.2
Ze	Labrador	SFA1	Middle Brook (Fox Cove)	0.000	0.000	0.200	0.563	1	0.313	51.9

Appendix 2. Biological characteristics data by rivers analyzed in the large salmon grouping.

Geography	Region	Zone	River	Proportion at smolt age				Presence age 6-7	Prop. female	Mean length
				2.000	3.000	4.000	5.000			
Aac	Maritime	SFA23	Mactaquac-W	0.522	0.452	0.025	0.001	0	0.768	77.2
Ab	Maritime	SFA23	Nashwaak-W	0.586	0.401	0.012	0.000	0	0.784	77.2
Ar	Maritime	SFA23	Big Salmon	0.461	0.526	0.009	0.000	0	0.761	72.9
Be	Maritime	SFA22	GASPEREAU	0.664	0.168	0.038	0.000	0	0.873	70.7
Bt	Maritime	SFA22	STEWIACKE	0.828	0.151	0.021	0.000	0	0.766	70.7
Ca	Maritime	SFA21	TUSKET	0.733	0.100	0.067	0.000	0	0.633	73.6
Cc	Maritime	SFA21	LAHAVE	0.896	0.065	0.000	0.000	0	0.779	73.5
Da	Maritime	SFA20	MUSQUODOBOIT	0.600	0.400	0.000	0.000	0	0.800	76.4
Dc	Maritime	SFA20	LISCOMB	0.967	0.033	0.000	0.000	0	0.711	72.3
Dd	Maritime	SFA20	ST MARYS	0.611	0.389	0.000	0.000	0	0.786	80.8
Dda	Maritime	SFA20	WEST RIVER ST MARYS	0.941	0.059	0.000	0.000	0	0.897	72.2
Eb	Maritime	SFA19	MIDDLE	0.229	0.650	0.121	0.000	0	0.675	74.9
Ec	Maritime	SFA19	BADDECK	0.205	0.795	0.000	0.000	0	0.826	75.7
Ed	Maritime	SFA19	SYDNEY	0.615	0.385	0.000	0.000	0	0.789	77.5
Ee	Maritime	SFA19	NORTH	0.113	0.744	0.144	0.000	0	0.786	73.0
Fa	Gulf	SFA18	Chetticamp	0.700	0.300	0.000	0.000	0	0.664	77.5
Fc	Gulf	SFA18	South	0.630	0.370	0.000	0.000	0	0.560	76.7
Fd	Gulf	SFA18	East River	0.760	0.240	0.000	0.000	0	0.690	77.0
Ga	Gulf	SFA16	Buctouche	0.664	0.336	0.000	0.000	0	0.777	78.4
Gb	Gulf	SFA16	Richibucto	0.591	0.395	0.014	0.000	0	0.643	75.6
Gc	Gulf	SFA16	Kouchibouguac	0.762	0.238	0.000	0.000	0	0.841	77.4
Gd	Gulf	SFA16	Miramichi	0.458	0.531	0.011	0.000	0	0.799	76.2
Ge	Gulf	SFA16	Tabusintac	0.348	0.652	0.000	0.000	0	0.784	79.1
Ha	Gulf	SFA15	Restigouche	0.266	0.696	0.039	0.000	0	0.613	82.8
Hc	Gulf	SFA15	Nepisiguit	0.909	0.090	0.000	0.000	0	0.611	85.6
Ia	Quebec	Q1	Cascapedia	0.075	0.623	0.302	0.000	0	0.511	95.7
Ib	Quebec	Q1	Petite riviere Cascapedia	0.033	0.828	0.139	0.000	0	0.474	78.1
Ic	Quebec	Q1	Bonaventure	0.030	0.455	0.459	0.031	0	0.705	76.5
Ja	Quebec	Q2	Grande Riviere	0.077	0.634	0.284	0.005	0	0.773	76.2
Jc	Quebec	Q2	Saint Jean	0.083	0.637	0.274	0.006	0	0.658	77.5
Ka	Quebec	Q7	Des Escoumins	0.407	0.593	0.000	0.000	0	0.671	78.2
Kb	Quebec	Q7	Laval	0.561	0.402	0.037	0.000	0	0.502	91.1
Kc	Quebec	Q7	Betsamites	0.909	0.090	0.002	0.000	0	0.719	79.8
Kd	Quebec	Q7	Godbout	0.230	0.674	0.092	0.004	0	0.675	75.2
Ke	Quebec	Q7	De la Trinite	0.143	0.724	0.129	0.004	0	0.883	75.8
Kf	Quebec	Q7	Aux Rochers	0.342	0.583	0.075	0.001	0	0.697	76.7
La	Quebec	Q8	Moisie	0.051	0.655	0.288	0.006	0	0.509	86.3
Lb	Quebec	Q8	Saint-Jean	0.053	0.652	0.290	0.004	0	0.566	77.4
Lc	Quebec	Q8	Mingan	0.085	0.662	0.252	0.000	0	0.550	79.1
Ld	Quebec	Q8	De la Corneille	0.106	0.867	0.027	0.000	0	0.535	70.4
Le	Quebec	Q8	Watshishou	0.004	0.608	0.351	0.037	0	0.551	74.0
Lf	Quebec	Q8	Petite riviere Watshishou	0.000	1.000	0.000	0.000	0	0.536	69.1
Lh	Quebec	Q8	Natashquan	0.000	0.428	0.552	0.021	0	0.743	75.6
Ma	Quebec	Q10	Bec-Scie	0.168	0.744	0.088	0.000	0	0.558	66.7
Mb	Quebec	Q10	Jupiter	0.021	0.720	0.254	0.005	0	0.709	69.0
Mc	Quebec	Q10	De la Chaloupe	0.121	0.783	0.093	0.003	0	0.826	70.3
Ne	Newfoundland	SFA13	Humber River	0.041	0.674	0.286	0.000	0	0.872	83.8
Nr	Newfoundland	SFA13	Rat Bay Brook	0.143	0.750	0.107	0.000	0	0.667	69.1
Nh	Newfoundland	SFA12	Middle Barachois River	0.069	0.931	0.000	0.000	0	0.939	67.1
Nj	Newfoundland	SFA13	Highlands River	0.137	0.829	0.035	0.000	0	0.679	81.3
Oc	Newfoundland	SFA11	Conne River	0.034	0.786	0.171	0.004	0	0.905	69.1
Od	Newfoundland	SFA11	Little River	0.377	0.507	0.116	0.000	0	0.844	70.1
Of	Newfoundland	SFA10	Pipers Hole Brook	0.000	0.438	0.500	0.063	0	1.000	66.3
Pc	Newfoundland	SFA10	Northeast River	0.000	0.684	0.316	0.000	0	0.833	65.9
Qb	Newfoundland	SFA9	Little Salmonier River	0.000	0.667	0.333	0.000	0	0.872	66.2
Qr	Newfoundland	SFA9	Rocky River	0.058	0.768	0.174	0.000	0	0.790	66.8
Qt	Newfoundland	SFA9	Northeast Brook	0.019	0.426	0.537	0.019	0	0.700	65.5
Qg	Newfoundland	SFA9	Biscay Bay River	0.000	0.692	0.308	0.000	0	0.643	65.7
Sa	Newfoundland	SFA5	Northwest River	0.067	0.533	0.400	0.000	0	0.688	63.5
Sb	Newfoundland	SFA5	Terra Nova River	0.000	0.250	0.600	0.150	0	0.962	67.0
Sc	Newfoundland	SFA5	Middle Brook	0.000	0.412	0.588	0.000	0	0.750	65.5
Ta	Newfoundland	SFA4	Gander River	0.000	0.309	0.602	0.089	0	0.691	68.3
Td	Newfoundland	SFA4	Exploits River	0.032	0.631	0.318	0.019	0	0.777	68.3
Va	Newfoundland	SFA14A	West River (WAB)	0.000	0.347	0.653	0.000	0	0.751	71.6
Vd	Newfoundland	SFA14A	Lomond River	0.100	0.900	0.000	0.000	0	0.800	69.7
Wa	Quebec	Q9	Bamamiou	0.000	0.583	0.417	0.000	0	0.778	78.0
Wc	Quebec	Q9	Saint-Paul	0.000	0.000	0.636	0.364	0	0.864	80.5
Xa	Labrador	SFA14B	Forteau Brook	0.050	0.250	0.650	0.050	0	0.500	71.6
Xb	Labrador	SFA14B	Pinware River	0.000	0.166	0.669	0.166	0	0.792	74.6
Yc	Labrador	SFA2	Eagle River	0.105	0.287	0.508	0.173	0	0.729	75.9
Yd	Labrador	SFA2	Sand Hill River	0.003	0.094	0.538	0.338	1	0.620	74.4
Za	Labrador	SFA1	Hunt River	0.000	0.222	0.457	0.296	0	0.709	75.3
Zc	Labrador	SFA1	Big River	0.000	0.125	0.750	0.125	0	0.542	73.8
Zd	Labrador	SFA1	Big Brook (Michaels River)	0.000	0.035	0.310	0.483	0	0.852	77.3

Appendix 3. Biological characteristics data by rivers analyzed in the combined small salmon and large salmon grouping.

Geography	Region	Zone	River	Proportion at smolt age				Prop. female		Mean length		Proportion of returns	
				2	3	4	5	in small	in large	of small	of large	Small	Maiden
Aaa	Maritime	SFA23	Mactaquac-W	0.507	0.468	0.024	0.000	0.076	0.768	57.1	77.2	0.548	0.950
Ab	Maritime	SFA23	Nashwaak-W	0.545	0.442	0.013	0.000	0.383	0.784	57.1	77.2	0.560	0.941
Ac	Maritime	SFA23	Big Salmon	0.506	0.484	0.009	0.000	0.624	0.761	54.5	72.9	0.582	0.598
Ba	Maritime	SFA22	GASPEREAU	0.556	0.338	0.031	0.000	0.540	0.873	54.2	70.7	0.576	0.932
Bb	Maritime	SFA22	STEWIACKE	0.690	0.304	0.001	0.000	0.679	0.765	55.0	70.7	0.694	0.693
Ca	Maritime	SFA21	TUSKET	0.450	0.155	0.048	0.000	0.459	0.633	56.0	73.6	0.742	0.986
Cc	Maritime	SFA21	LAHAVE	0.867	0.110	0.001	0.000	0.379	0.779	54.1	73.5	0.824	0.901
Da	Maritime	SFA20	MUSQUODOBOIT	0.690	0.273	0.037	0.000	0.200	0.800	58.6	76.4	0.405	0.982
Dc	Maritime	SFA20	USCOMB	0.884	0.080	0.008	0.000	0.593	0.711	53.5	72.3	0.873	0.817
Dda	Maritime	SFA20	WEST RIVER ST MARYS	0.806	0.191	0.000	0.000	0.626	0.897	54.8	72.2	0.866	0.928
Eb	Maritime	SFA19	MIDDLE	0.147	0.774	0.080	0.000	0.000	0.675	56.0	74.9	0.235	0.954
Fa	Gulf	SFA18	Cheticamp	0.706	0.294	0.000	0.000	0.000	0.664	55.6	77.5	0.189	0.946
Fb	Gulf	SFA18	Margaree	0.567	0.410	0.022	0.001	0.166	0.813	56.2	82.7	0.312	0.923
Fc	Gulf	SFA18	South	0.430	0.570	0.000	0.000	0.030	0.560	54.4	76.7	0.170	0.900
Fd	Gulf	SFA18	East River	0.360	0.640	0.000	0.000	0.050	0.690	57.5	77.0	0.110	0.870
Ga	Gulf	SFA16	Buctouche	0.555	0.426	0.019	0.000	0.106	0.777	56.3	78.4	0.372	0.837
Gd	Gulf	SFA16	Miramichi	0.421	0.562	0.016	0.000	0.201	0.799	53.9	76.2	0.670	0.928
Ge	Gulf	SFA16	Tabusintac	0.266	0.715	0.019	0.000	0.060	0.784	56.9	79.1	0.466	0.903
Ha	Gulf	SFA15	Restigouche	0.251	0.712	0.037	0.000	0.071	0.613	53.8	82.8	0.453	0.935
Hb	Gulf	SFA15	Nepisguit	0.887	0.112	0.000	0.000	0.055	0.611	54.5	85.6	0.499	0.910
Jc	Quebec	Q2	Saint-Jean	0.063	0.636	0.294	0.008	0.018	0.658	55.1	77.5	0.274	0.957
Ke	Quebec	Q7	De la Trinité	0.127	0.729	0.142	0.001	0.106	0.883	55.2	75.8	0.640	0.945
Ma	Quebec	Q10	Bec-Scie	0.119	0.745	0.132	0.004	0.183	0.558	51.2	66.7	0.507	0.979
Mb	Quebec	Q10	Jupiter	0.027	0.662	0.306	0.005	0.145	0.709	50.6	69.0	0.460	0.969
Na	Newfoundland	SFA13	Humber River	0.020	0.471	0.493	0.016	0.525	0.872	55.0	83.8	0.905	0.970
Ne	Newfoundland	SFA13	Flat Bay Brook	0.052	0.748	0.200	0.000	0.628	0.667	53.6	89.1	0.919	0.820
Nh	Newfoundland	SFA13	Middle Barachois River	0.150	0.755	0.096	0.000	0.539	0.939	51.9	67.1	0.878	0.898
Nj	Newfoundland	SFA13	Highlands River	0.077	0.759	0.161	0.003	0.514	0.679	54.4	81.3	0.625	0.879
Oc	Newfoundland	SFA11	Conne River	0.026	0.763	0.205	0.005	0.752	0.905	51.5	69.1	0.944	0.907
Od	Newfoundland	SFA11	Little River	0.192	0.694	0.109	0.003	0.788	0.844	52.2	70.1	0.892	0.847
Pb	Newfoundland	SFA10	Pipers Hole Brook	0.054	0.577	0.354	0.015	0.830	1.000	53.4	66.3	0.861	0.757
Pc	Newfoundland	SFA10	Northeast River	0.126	0.726	0.136	0.012	0.913	0.833	53.8	65.9	0.883	0.801
Qb	Newfoundland	SFA9	Little Salmonier River	0.025	0.748	0.224	0.004	0.906	0.872	55.2	66.2	0.807	0.753
Qc	Newfoundland	SFA9	Rocky River	0.128	0.725	0.142	0.006	0.799	0.790	56.1	66.8	0.822	0.705
Qf	Newfoundland	SFA9	Northeast Brook	0.003	0.466	0.489	0.042	0.849	0.700	55.1	65.5	0.839	0.826
Qg	Newfoundland	SFA9	Biscay Bay River	0.081	0.653	0.259	0.007	0.726	0.643	52.9	65.7	0.949	0.818
Sa	Newfoundland	SFA5	Northwest River	0.036	0.451	0.432	0.076	0.841	0.688	53.9	63.5	0.781	0.701
Sb	Newfoundland	SFA5	Terra Nova River	0.006	0.517	0.430	0.045	0.755	0.952	51.7	67.0	0.818	0.732
Sc	Newfoundland	SFA5	Middle Brook	0.006	0.508	0.452	0.033	0.763	0.750	52.4	65.5	0.941	0.875
Tb	Newfoundland	SFA4	Gander River	0.004	0.367	0.572	0.055	0.766	0.691	53.7	68.3	0.891	0.839
Td	Newfoundland	SFA4	Exploits River	0.020	0.621	0.333	0.025	0.768	0.777	51.7	68.3	0.947	0.899
Va	Newfoundland	SFA14A	West River (WAB)	0.001	0.350	0.611	0.036	0.781	0.751	52.6	71.6	0.957	0.967
Vd	Newfoundland	SFA14A	Lomond River	0.131	0.830	0.039	0.000	0.570	0.800	51.5	69.7	0.885	0.954
Xa	Labrador	SFA14B	Forteau Brook	0.000	0.119	0.667	0.201	0.639	0.500	54.2	71.8	0.704	0.910
Xb	Labrador	SFA14B	Pinware River	0.000	0.050	0.591	0.339	0.357	0.792	53.3	74.6	0.847	0.986
Yd	Labrador	SFA2	Sand Hill River	0.001	0.069	0.487	0.387	0.385	0.620	54.4	74.4	0.884	0.978
Zd	Labrador	SFA1	Big Brook (Michaels River)	0.000	0.050	0.199	0.440	0.191	0.862	55.2	77.3	0.825	0.988